A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

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With one plate

Subgenus II. **Kirganelia** (Juss.) Webster, Jour. Arnold Arb. **37**: 344. 1956.

Kirganelia Juss. Gen. Pl. 387. 1789.
Phyllanthus sect. *Kirganelia* (Juss.) Muell. Arg. Linnaea **32**: 11. 1863; DC. Prodr. **15**(*2*): 341. 1866.

Trees, shrubs, or herbs with phyllanthoid branching; monoecious or dioecious. Male flower: calyx-lobes 5 or 6; disk of 5 or 6 segments; stamens 5 or 6, free or rarely united by the filaments; anthers dehiscing vertically or horizontally; pollen grains more or less globose, colporate. Female flower: calyx-lobes 5 or 6; disk usually as in male; ovary of 3–12 carpels; styles mostly bifid, sometimes entire, often thickened and fleshy. Fruit capsular or baccate; seeds trigonous.

This subgenus, typified by sect. *Anisonema*, comprises about 35 species in several closely related sections. None is native to the New World, and most of the species are restricted to Africa and the Mascarene islands, although they also occur in India, China, Japan, Malaysia, and Australia.

Subgenus *Kirganelia* includes not only some of the most primitive of the species with phyllanthoid branching but also a number of highly specialized herbaceous species (in sect. *Floribundi*) which form a transition to the herbaceous representatives of sect. *Phyllanthus*. A significant indication of the relative primitiveness of this subgenus is the great floral variability.

In the West Indies subgenus *Kirganelia* is represented by two very different species belonging to two different sections.

KEY TO THE SECTIONS

Fruit capsular; stamens 5, filaments free ..... 2. **Floribundi**
Fruit baccate; filaments connate in two groups ..... 3. **Anisonema**

Sect. 2. **Floribundi** Pax & Hoffm. Pflanzenw. Afr. 3(*2*): 22. 1921.

Trees, shrubs, or herbs with phyllanthoid branching; leaves (in ours) membranous, not over 2 cm. long. Monoecious or dioecious, flowers in abbreviated unisexual or bisexual axillary cymules. Male flower: calyx-lobes 5, small, uninerved; disk of 5 discrete segments; stamens 5, filaments free; anthers dehiscing vertically or horizontally; pollen grains subglobose, 4-colporate (in *P. tenellus*), finely reticulate. Female flower: pedicel long

* Continued from volume XXXVII, p. 359.

and capillary; disk cupulate; ovary of 3 carpels, smooth; styles free or united beneath, bifid, the style-branches slender or dilated. Capsule oblate, the valves membranous and veiny; seeds trigonous, smooth or rugulose.

TYPE SPECIES: *Phyllanthus floribundus* Muell. Arg. [= *P. muelleranus* Exell].

This exclusively Old World section of perhaps 10 to 15 species is best developed in Africa; only one species, *P. tenellus* Roxb., has become naturalized in America. The group as here defined has a different circumscription from that of Pax and Hoffmann. They included in sect. *Floribundi* those species previously classified in sect. *Menarda* which had fascicles of inflorescences at the nodes. Consequently, they retained *P. tenellus* and its relatives, which lack fascicled inflorescences, in sect. *Menarda*. Unfortunately, however, even the emended sect. *Menarda* of Pax and Hoffmann contains discordant elements. The type species, *P. cryptophilus* (A. Juss.) Muell. Arg., contrasts with all of the other species by virtue of its non-phyllanthoid branching and opposite leaves of peculiar texture. In the present circumscription, therefore, sect. *Menarda* is restricted to *P. cryptophilus* and a few other species of Madagascar, while all of the other species placed in the group by Mueller and by Pax are removed to sect. *Floribundi*. The latter, as thus constituted, is polymorphic and perhaps could be further divided, but any additional change in its definition must await careful study of the African species.

The description of the section is based primarily on the single species in the West Indies, *P. tenellus*, and therefore cannot be regarded as authoritative for the entire section. The relationships of sect. *Floribundi* are perhaps closest to sect. *Chorisandra* (Wight) Muell. Arg. The type species of the latter group, *P. pinnatus*,[11] agrees in having a crustaceous capsule, slender bifid styles, and free stamens (though 6 in number instead of 5). However, the seeds of *P. pinnatus* are very different, being hollowed out at the hilum. It is possible that further study may result in the merging of the two sections. On the other hand, sect. *Floribundi* is doubtless rather closely related to sect. *Anisonema*. Although the West Indian representatives of both groups are very easy to distinguish, there are species in Africa and Madagascar which seem to defy sectional limits; and future revision in the boundaries of these two groups may perhaps be required, although they are so distinctive on the whole that there would appear to be little advantage in merging them.

4. **Phyllanthus tenellus** Roxb. Fl. Ind. [ed. 2] 3: 668. 1832; Muell. Arg. in DC. Prodr. **15**(2): 337. 1866; Hook. f. in Hook. Icon. 1569. 1887. (TEXT-FIG. 6; PLATE I, *fig.* 3).

Phyllanthus corcovadensis Muell. Arg. Fl. Bras. **11**(2): 30, *pl. 6, fig. 2.* 1873.
Diasperus tenellus (Roxb. "em.") O. Ktze. Rev. Gen. **2**: 601. 1891.

[11] **Phyllanthus pinnatus** (Wight) comb. nov.; *Chorisandra pinnata* Wight, Icon. Pl. Ind. Or. **6**: 13, *pl. 1994.* 1853; *Phyllanthus wightianus* Muell. Arg.

Phyllanthus minor Fawc. & Rend. Jour. Bot. **57**: 65–66. 1919.
Phyllanthus nummulariaefolius sensu Croizat, Torreya **42**: 14. 1942; non *P. nummulariaefolius* Poir.

Erect annual herb, typically with a single main (primary) stem c. 2 — 5 dm. high, 1.5 — 2 mm. thick, olivaceous or stramineous, smooth, terete or roundly angled, sometimes channelled; internodes mostly 10 — 35 mm. long. Cataphylls: stipules lanceolate, 0.7 — 1 mm. long, 0.2 — 0.3 mm. broad, acuminate, not auriculate, entire, olivaceous or reddish with rather narrow scarious margins; blade linear-lanceolate, 0.6 — 0.9 mm. long, attenuate-acuminate, similarly colored. Penultimate branches well developed in vigorous individuals (becoming up to 2 dm. long) or quite suppressed in smaller plants. Deciduous branchlets ascending, mostly 5 — 15 cm. long, 0.25 — 0.5 mm. thick, olivaceous, smooth or scabridulous, somewhat angled, with mostly 10 — 25 leaves; first internode (5–) 8 — 15 (–25) mm. long, median internodes c. 3 — 6 mm. long. Leaves: stipules lanceolate, 0.7 — 1.1 mm. long, acuminate, not auriculate, entire, olivaceous or reddish with white scarious margins. Petiole 0.5 — 0.8 mm. long. Leaf-blades membranous, smooth on both sides, mostly broadly elliptic to obovate, (6–) 10 — 20 (–24) mm. long, (4–) 5 — 9 (–11) mm. broad, acute or obtuse at the tip, acute to rounded at the base; above bright or dark green with the midrib and arching laterals (5 — 8 on a side) slightly raised; beneath pallid, the midrib raised, the laterals forming with the tertiary veinlets a fine reticulum; margins smooth.

Monoecious; all axils of deciduous branchlets usually floriferous. Proximal axils bisexual, the 1 or 2 female flowers beneath, the 2 or 3 male flowers above; distalmost cymules usually reduced to a single female flower.

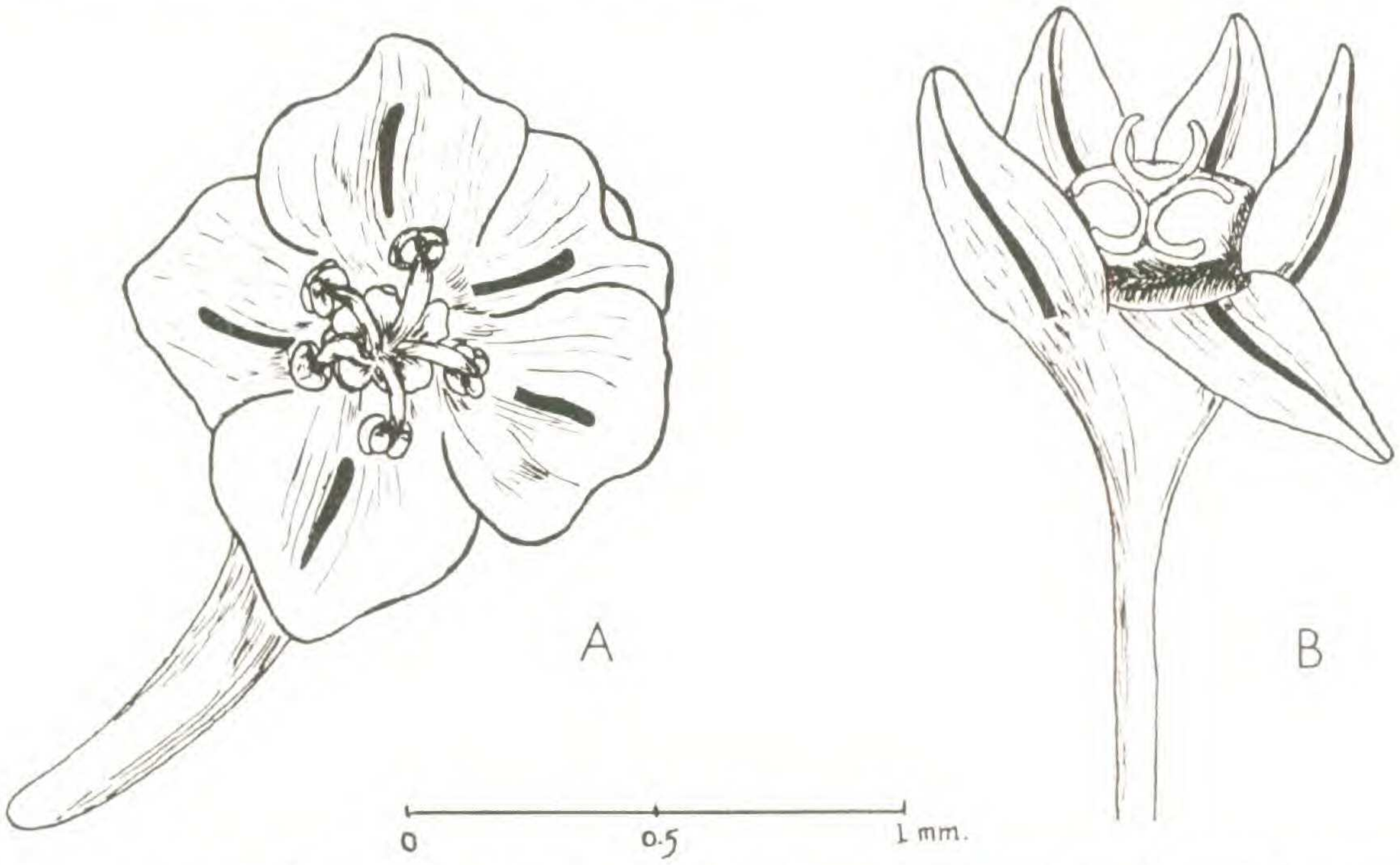
Male flower: Pedicel filiform, 0.5 — 1.5 mm. long. Calyx-lobes 5, imbricate at anthesis, subequal, broadly elliptic or obovate, c. 0.4 — 0.6 (–0.7) mm. long, 0.5 — 0.7 (–0.8) mm. broad, acute to rounded at the tip, entire, membranous, whitish except for the narrow green unbranched midrib. Disk-segments 5, broadly cuneate, thin, entire, c. 0.2 mm. across. Stamens 5, alternate with the disk-segments; filaments free, filiform, c. 0.2 — 0.3 mm. long, bent near the top; anthers reniform, 0.15 — 0.25 mm. broad, the long axis almost or quite horizontal; anther-sacs divergent, the slits confluent near the apex of the anther; pollen grains 17.5 — 19 μ in diameter, 4-colporate, the colpi not meeting at the poles.

Female flower: Pedicel capillary and flexuous, (2.5–) 3 — 5 (–7) mm. long, olivaceous (or reddish below), smooth and terete, dilated into a cylindrical pulvinus at the base and often bent at the pulvinar apex. Calyx-lobes 5, spreading at anthesis, triangular-ovate, 0.6 — 0.8 mm. long, 0.3 — 0.5 mm. broad, narrowed to an acute tip (in fruit reflexed, elliptic or oblong, and obtuse), entire, membranous, whitish except for the narrow green unbranched midrib. Disk patelliform, fleshy but thin, the margins undulate. Styles free, horizontally appressed, spreading, c. 0.25

mm. long, very slender, bifid to ⅔ parted, the branches divaricately spreading, the tips subcapitate.

Capsule oblate, rounded-trigonous, c. 1 mm. high, 1.7 — 1.9 mm. in diameter, greenish, obscurely reticulate-veiny. Seeds trigonous, c. 0.9 mm. long, 0.7 — 0.75 mm. radially and tangentially, light brown, densely pebbled on all sides with rounded processes; hilum linear-oblong.

Collected May through December, but perhaps flowering throughout the year where conditions are favorable.



TEXT-FIG. 6. *Phyllanthus tenellus* Roxb. (*Harris 12204*[GH]). A, male flower; B, female flower.

TYPE: Botanic Gardens, Calcutta, *Wallich 7892A ex p.* (K, HOLOTYPE). According to Roxburgh, the species was introduced from Mauritius in 1802 by Captain Tennant. However, Baker (Fl. Maur. 310. 1873) was unable to find a single Mauritian specimen of the plant. Since it appears improbable that so aggressive a weed as *P. tenellus* could have been overlooked by visitors to that island, the species was most likely collected in one of the other Mascarene islands. De Cordemoy (Fl. Reunion 346. 1895), for instance, has recorded it as very common everywhere in Reunion.

DISTRIBUTION: the typical var. *tenellus* (var. *roxburghii* of Mueller), native to the Mascarene islands, has been introduced into the southeastern United States, the West Indies, Brazil, and doubtless other areas of the New World.

JAMAICA. St. ANN: Mt. Diablo, road to Hollymount, *Webster & Wilson 5016* (A, JAM, MICH). CLARENDON: 0.5 mile NW of Kupuis, *Proctor 10331* (GH). ST. ANDREW: Hope Grounds, in shady places, alt. 700 ft., *Harris 12123* (GH, NY, US), *12157* (NY, US), *12208* (GH, JAM, MT, NY, US; *P. minor* based on all three Harris collections).

LESSER ANTILLES. GUADELOUPE: Camp-Jacob, Choisy, Bagatelle, *Duss 2442, 3557* (NY); Montebello, *Questel 440* (US); between Goyave and Petit Bourg, Bailly, *Rodriguez 4390, 3935bis* (P). DOMINICA: Sylvania Estate, cleared forest land, *Hodge 573* (NY). MARTINIQUE: Morne-Rouge, Carbet, Fonds St. Denis, *Duss 47a* (NY, US); 1847, *Hahn 374* (A, P); environs St. Pierre, *Hahn 585* (G); St. Pierre, *Steinheil 24 ex p.* (P, mixed with *P. amarus*). GRENADA: under nutmegs, Grenville Vale, St. George Parish, *Hunnewell 19476* (GH).

Croizat (loc. cit.) has followed the example of Leandri (Not. Syst. 7: 168–169. 1939) in reducing *P. tenellus* to a synonym of *P. nummulariaefolius* Poir. As Leandri remarks, leaf size and pedicel length are excessively variable in this species-group, and the distinguishing characters proposed by Mueller are not convincing. Nevertheless, after examination of the holotype of *P. nummulariaefolius* (Herb. Lam., P) and of some Madagascar specimens cited by Leandri (*Humbert 5848, 6122*; A), I believe that these specimens represent a species closely allied to but distinct from *P. tenellus*. The calyx-lobes of the male flower of *P. nummulariaefolius* are about 1 mm. long, or almost twice the length of those of *P. tenellus;* and the pedicel of the male flower is about 3 — 6 mm. long in the former species, while in our West Indian plants it is never over 1.5 mm. in length. The leaf-shape also appears to be somewhat different in the two species, the blade of *P. nummulariaefolius* being rhombic- or suborbicular-obovate and rather abruptly contracted to a point, while that of *P. tenellus* is obovate and smoothly obtuse or rounded at the tip. Fawcett and Rendle were correct in noting the differences between the Jamaican plant and *P. nummulariaefolius*, but did not realize that the former was conspecific with *P. tenellus*.

As Leandri has observed (in lit.), the species of the complex to which *P. nummulariaefolius* and *P. tenellus* belong are at present so poorly defined that a careful monographic revision of them will be necessary before there can be any confidence with regard to species delimitation. The status of the six additional varieties of *P. tenellus* described by Mueller, as well as such closely allied species as *P. capillaris* Schum., must therefore be regarded as provisional.

The earliest record of *P. tenellus* from the West Indies is apparently the collection made on Martinique in 1839 by Steinheil. Judging from its rapid spread over Florida and Georgia within about twenty years of its introduction into the United States, it probably dispersed rapidly over the Lesser Antilles once given a foothold there. Its present naturalized area in the West Indies is strikingly parallel to that of another Old World congener, *P. urinaria*; both are widespread in Jamaica and the Lesser Antilles but have failed to become established on Cuba, Hispaniola, or Puerto Rico. The reasons for this are not entirely clear, for there are plenty of mesophytic habitats in the latter group of islands which would be attractive to the two species. The absence of *P. tenellus* from these islands is particularly surprising in view of the aggressively weedy nature of the plant; as Croizat remarks, it will quickly overrun a greenhouse if given a chance.

This "aggressive" nature of *P. tenellus* is largely due to the rapidity of growth and reproductive maturation of the plant. A seedling when only a few centimeters high is already producing explosively dehiscent capsules, and deciduous branchlets which have only two or three leaves unrolled will already have a completely developed fruit.

Phylogenetically *P. tenellus* is of considerable interest, because it and its allies appear to represent the link connecting the shrubby species of sect. *Floribundi* with the herbaceous species of sect. *Phyllanthus*. In its usual growth habit it agrees with some of the latter so closely that it can easily be confused with them. However, when grown in the greenhouse *P. tenellus* betrays its less specialized nature, for it may persist three years or more, become definitely shrubby at the base, and branch many times above. Indeed, Roxburgh reported that his original plant in the gardens at Calcutta grew to be a shrub 3.5 feet high. In contrast, the annual herbaceous species of sect. *Phyllanthus* such as *P. amarus* live only about a year or less even when pampered in the greenhouse.

Although the general aspect of *P. tenellus* is that of many species of sect. *Phyllanthus*, there is no reason why it should be confused with them. The long pendent capillary fruiting pedicels of *P. tenellus* are diagnostic, and of course no other herbaceous West Indian species has male flowers with five free stamens.

Sect. 3. **Anisonema** (A. Juss.) Griseb. Fl. Br. W. Ind. 34. 1859.

Kirganelia Juss. Gen. Pl. 387. 1789.
Anisonema A. Juss. Euphorb. Tent. 19, *pl. 4, fig. 11*. 1824.
Kirganelia sect. *Anisonema* (A. Juss.) Baill. Etud. Gen. Euphorb. 613–614. 1858.
Kirganelia sect. *Anisonemopsis* Baill. op. cit. 614.
Kirganelia sect. *Eukirganelia* Baill. ibid.
Phyllanthus sect. *Kirganelia* (Juss.) Muell. Arg. Linnaea **32**: 11, 1863; DC. Prodr. **15**(2): 341. 1866.
Phyllanthus sect. *Typophyllanthus* subsect. *Kirganelia* (Juss.) O. Ktze. in Post & Kuntze, Lexicon 434. 1904.

Shrubs or small trees with the habit of *Breynia;* leaves chartaceous with rather conspicuous venation. Monoecious; flowers long-pedicelled, in bisexual cymules, the female flowers one or few, the males more numerous. Male flower: Calyx-lobes 5 or 6, unequal, entire; disk of discrete segments; stamens 5, unequal, in two sets: the inner connate with long filaments, the outer discrete with shorter filaments, filaments all free in some extralimital species fide Mueller; anthers extrorse, dehiscing longitudinally, the anther-sacs not confluent; pollen grains globose, tricolporate, finely reticulate. Female flower: Calyx-lobes 5 or 6, unequal, entire; disk of discrete or paired contiguous segments; ovary smooth, of 3 — 12 carpels; styles more or less bifid, often thickened and fleshy, more or less connivent. Fruit capsular or baccate; seeds trigonous.

TYPE SPECIES: *Phyllanthus reticulatus* Poir.

This section of about 10 Old World species is best distinguished by the curious androecium of five stamens unequally united into two sets. *Anisonema* and *Kirganelia* were distinguished by A. Jussieu (as genera) and by Baillon (as sections) on the basis of the number of locules in the ovary. However, the type species of the two groups, *P. reticulatus* Poir. and *P. casticum* Willem., agree in having the characteristic androecium, and Mueller was quite justified in combining them. Possibly he did not go far enough, for some of the species he included in his sect. *Kirganelia*, such as *P. physocarpus*, could as easily be placed in his sect. *Menarda* (i.e., sect. *Floribundi*).

The taxonomic difficulties attendant with sectional limits here are aggravated by the nomenclatural vagaries of typification. Mueller (DC. Prodr. **15**(2): 341. 1866) and Pax and Hoffmann (Naturl. Pflanzenfam. **19c**: 62. 1931) applied the epithet *Kirganelia* to the present section. It is true that *Kirganelia* is the oldest generic name, but as a sectional name in *Phyllanthus* it must yield priority to *Anisonema*. This, as it turns out, is fortunate, because the type species of *Kirganelia* (*P. casticum*) has such a broad latitude of variation that among its own subspecies it nearly bridges the gap with sect. *Flueggeopsis*. All these nomenclatural difficulties are symptoms of an unstable taxonomy. When a monographic study can be made of subg. *Kirganelia*, it is likely that several of these closely related sections will be combined.

In the West Indies sect. *Anisonema* is represented only by a single introduced species.

5. **Phyllanthus reticulatus** Poir. Enc. Method. **5**: 298. 1804 (as *P. reticulata*); Muell. Arg. in DC. Prodr. **15**(2): 345. 1866. (TEXT-FIG. 7).

Phyllanthus jamaicensis Griseb. Fl. Br. W. Ind. 34. 1859 (for the remainder of the complicated synonymy see Mueller loc. cit.).

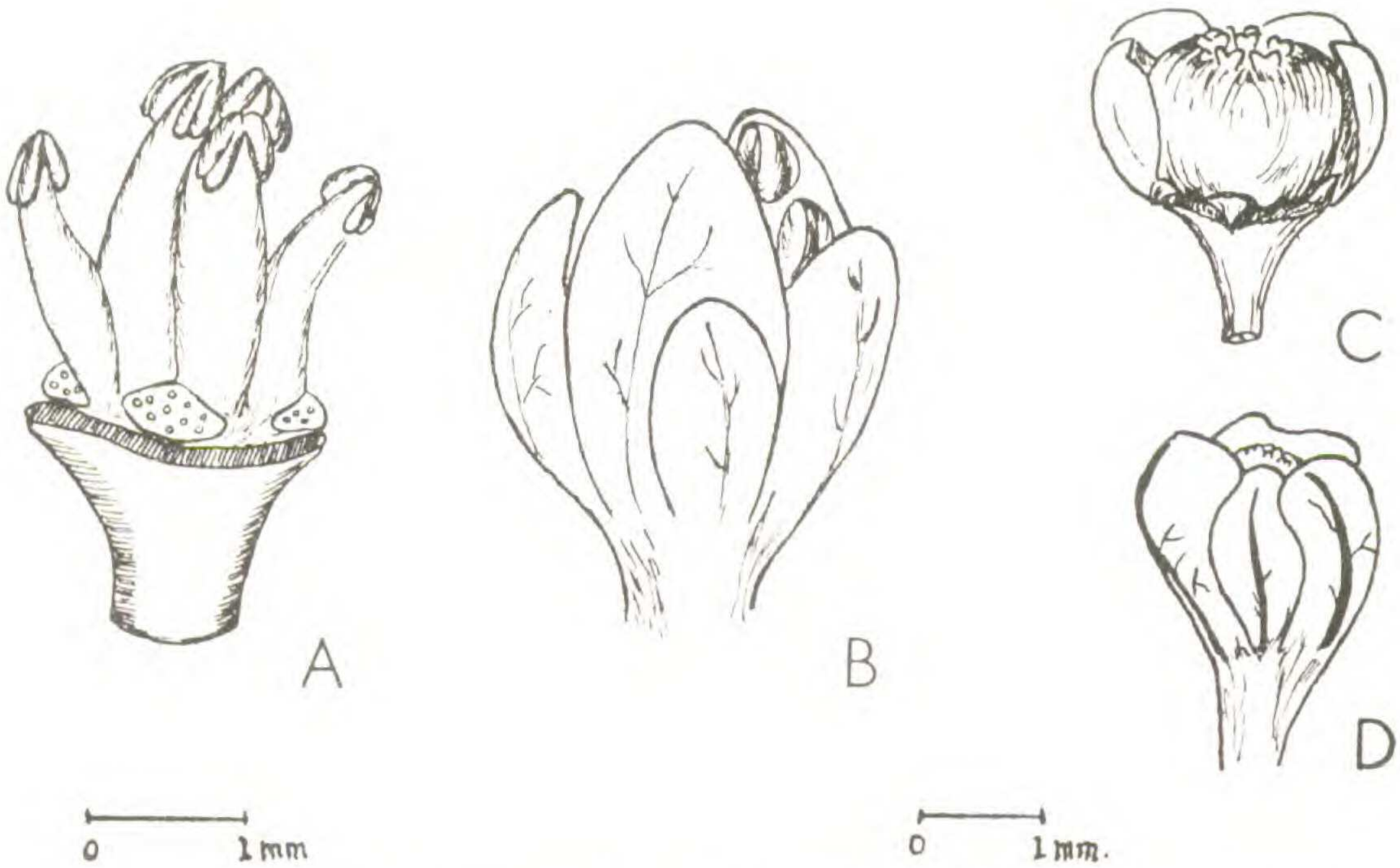
A much-branching shrub or small bushy tree up to 4 m. high; branches of current year smooth and glabrous, somewhat angled, dark brown, 2 — 3 mm. thick, with internodes mostly 1 — 2 cm. long. Cataphylls: stipules triangular, (1.2–) 1.5 — 1.7 mm. long, mostly 1 — 1.4 mm. broad, acuminate, truncate at the base, subcarnose, dark blackish brown, margins ciliate; blade lanceolate, (1.1–) 1.3 — 1.7 mm. long, 0.4 — 0.9 mm. broad, acuminate, similar in texture, ciliate. Deciduous branchlets steeply ascending, (8.5–) 10 — 20 (–25) cm. long, 0.5 — 1 mm. thick, dark brown, somewhat angled, quite smooth, with (10–) 13 — 16 (–25) leaves; internodes mostly 7 — 13 mm. long. Leaves: stipules lanceolate, (0.8–) 1 — 1.4 (–1.6) mm. long, 0.5 — 0.7 mm. broad, acuminate, truncate at the base, margins ciliate, olivaceous turning more or less dark brownish, rather scarious. Petioles smooth, plano-convex, 1.5 — 2.5 mm. long. Leaf-blades chartaceous, smooth on both surfaces, elliptic, (13–) 15 — 25 (–32) mm. long, (9–) 10 — 15 mm. broad, obtuse or rounded at the tip, cuneate at the base; midrib and laterals (5 — 7 on a side) raised and conspicuous

particularly beneath, where they form with the tertiaries a conspicuous reticulum; margins not thickened, more or less plane.

Monoecious; most deciduous branchlets floriferous; first 1 or 2 (rarely more) proximal nodes barren, succeeding ones with bisexual cymules; female flower solitary or sometimes paired in each cymule, male flowers up to 8.

Male flower: pedicel capillary, 5 — 10 mm. long. Calyx-lobes 5 or 6, unequal, imbricate in 2 or 3 series, c. 2 — 2.5 mm. long, the outer oblong or obovate, rounded at the tip and c. 0.7 — 1.2 mm. broad, the inner nearly orbicular, subtruncate at the tip and c. 1.3 — 1.8 mm. broad; lobes of both series entire, with simple or sparsely branched midrib, somewhat thickened adaxially at the base; margins thin and scarious. Disk-segments 5, broadly ovate or reniform, thin, subcarnose, erect, entire, foveolate, 0.35 — 0.5 mm. across. Stamens 5, erect, in two sets: three with longer filaments (0.7 — 1.3 mm. long) coherent in a central column, two with shorter filaments (0.3 — 0.8 mm. long) free and displaced to the sides — or vice versa (i.e., two stamens central and coherent with three shorter ones peripheral and more or less free); filaments fusiform, often conspicuously thicker than the anthers, 0.25 — 0.5 (–0.6) mm. broad. Anthers erect, triangular, c. 0.3 — 0.5 mm. long and broad; anther-sacs divergent, dehiscing longitudinally, discrete, the slits apically contiguous but not confluent; pollen grains c. 14 — 17 μ in diameter, tricolporate, colpi conspicuously bordered and meeting at the poles, reticulum rather coarse.

Female flower: pedicel subterete, slender, (4–) 5 — 8 mm. long. Calyx-



TEXT-FIG. 7. *Phyllanthus reticulatus* Poir. (*Webster & Wilson 5237*[A]). A male flower with calyx-lobes removed to show androecium and disk; B, male flower entire; C, female flower with two calyx-lobes removed to show ovary and styles; D, female flower entire (B, C, and D to the same scale).

lobes 5 or 6, erect and closely investing the ovary, unequal, in 2 or 3 series (the innermost segment completely overlapped by the others); the outer oblong-elliptic, c. 1.6 — 1.8 mm. long and 0.9 — 1.2 mm. broad, strongly carinate, midrib simple or sparsely branched; the inner nearly orbicular, c. 1.4 — 1.7 mm. long, 1.2 — 1.5 mm. broad, carinate or plane, the midrib sparingly branched. Disk-segments 5 or 6, often subpaired, oblong or cuneate, somewhat thickened and fleshy, c. 0.3 — 0.4 mm. broad, obscurely foveolate. Ovary oblate-spheroidal, smooth, not perceptibly sulcate; carpels mostly 9 or 10 (in West Indian material); styles c. 0.25 mm. long, bifid, thickened and fleshy, free but inflexing and connivent over the top of the ovary as an irregular furrowed mass of stigmatic tissue.

Mature fruit baccate, globose or oblate, c. 4 — 6 mm. in diameter, shiny black with dark purplish pulp. Seeds trigonous (when in pairs), c. 1.6 — 2 mm. long, blackish, colliculose; hilum shallow, less than 0.5 mm. across.

Flowering and fruiting March to July, and probably later in the year as well.

TYPE: Herb. Lamarck (P, HOLOTYPE). The type sheet contains a mixture of *P. reticulatus* and a species of *Breynia*.

DISTRIBUTION: Widespread in the Old World from West Africa to India, Ceylon, China, Indonesia, the Philippines, and Queensland; introduced into the West Indies.

JAMAICA. common, Oct. 1857, *Wilson* (GOET, HOLOTYPE of *P. jamaicensis*); donne par Sir W. Hooker, 1845 (P); center and east Jamaica, thickets and river banks, *Velez 3781* (US). ST. THOMAS: shores of Plantain Garden River, *Harris & Britton 10677* (NY, US), *Webster & Wilson 5237* (A, JAM, MICH); Bath, *Orcutt 2013* (US); fields, Holland Bay, *Britton 4067* (NY).

LESSER ANTILLES. ST. VINCENT: *Caley* (P); Liberty Lodge, alt. 500 ft., *Eggers 6769* (GOET, P, US); thickets near houses, hills near Kingstown, alt. 800 ft., *H. H. & G. W. Smith 872* (NY).

This introduced Old World plant is readily recognizable by virtue of its peculiar androecium and baccate fruit, and cannot be mistaken for any native West Indian species. Although in its native range *P. reticulatus* is extremely variable, the specimens from the West Indian populations all represent the glabrous form, var. *glaber* of Mueller. Poiret's type specimen is definitely pubescent, but since — as pointed out by J. D. Hooker (Fl. Br. Ind. **5**: 288. 1887) — the pubescent and glabrous forms occur indiscriminately together, it does not seem worthwhile to designate the form in the West Indies with a varietal name. *Phyllanthus jamaicensis* Griseb. was described under the mistaken impression that the plant was endemic to Jamaica. However, the specimen collected by Wilson and now in the Herbarium Grisebachianum (GOET) can be matched by many sheets from the Old World, and shows no significant differences.

The only striking peculiarity of the West Indian specimens of *P. reticulatus* appears to be their infertility. Only two fruits were observed on a copiously flowering plant seen in the field at the Plantain Garden River, Jamaica (*Webster & Wilson 5237*), and each of these contained but a single well-developed seed. In contrast, many specimens from the Old World — e.g., *Merrill Species Blancoanae 674* (A) — have numbers of fruits, each of which have 12 — 16 mature seeds.

J. J. Smith (Add. Fl. Arb. Jav. 12: 67. 1910) describes the seeds of a living plant of *P. reticulatus* as greenish, with "testae strato exteriore succoso, strato interiore duro." If the seed-coat of *P. reticulatus* is actually fleshy, this would be an extremely interesting indication of a close relationship between this plant and species of *Glochidion* and *Breynia*. However, judging from the seeds of *Webster & Wilson 5237* and *Merrill 674*, the seed-coat could at most be called slightly fleshy. The outer seed-coat is scarcely thicker than the inner and certainly appears no different from that of many typical species of *Phyllanthus*. Furthermore, since there is no hilar indentation in *P. reticulatus* and the embryo is straight, it does not appear that this species represents a very close approach to the seed structure of *Glochidion*.

Subgenus III. **Cicca** (L.) Webster, Jour. Arnold Arb. 37: 344. 1956.

Cicca L. Mant. 17. 1767.

Trees or rarely shrubs with phyllanthoid branching. Monoecious or dioecious, inflorescences commonly fascicled or cauliflorous. Male flower: calyx-lobes 4 — 6; disk of 4 — 6 segments or absent; stamens 3 or 4 (rarely 2 or 5), filaments free; anthers dehiscing more or less vertically; pollen grains 3-colporate. Female flower: calyx-lobes 4 — 6; disk cupuliform or absent; ovary of 2 — 4 carpels; styles bifid, free or shortly connate at the base. Fruit indehiscent, woody or drupaceous; seeds 1 or 2 in each fertile locule.

This subgenus contains some of the most distinctive groups in the genus, and it is not surprising that at times sects. *Cicca*, *Aporosella*, and *Emblica* have been recognized as generically distinct from *Phyllanthus*. The accumulation of further evidence from such fields as wood anatomy and cytology may possibly justify the maintenance of one or more of these groups as an independent genus. However, at the present time they seem best regarded as divergent sections of *Phyllanthus*, especially since sect. *Ciccopsis* would appear to at least partially bridge the gap between sect. *Cicca* and typical representatives of sect. *Kirganelia*. It should also be pointed out here that the inclusion of sect. *Emblica* in the present subgenus is quite possibly contrary to natural relationship, and is justified in this West Indian study on the grounds of convenience.[12] With the exception of sect. *Emblica*, the species of subg. *Cicca* are all native to the New World.

[12] The description of the subgenus applies only to the American representatives and does not refer to the special features of sect. *Emblica*.

KEY TO THE SECTIONS

1. Calyx-lobes 6; male flower with 3 stamens, the filaments free; leaves elliptic, obtuse or rounded at the tip. ..... 4. **Ciccopsis**
1. Calyx-lobes 4 or if 6 then filaments of stamens united; leaves otherwise.
   2. Fruit indehiscent; calyx-lobes usually 4; leaves elliptic to ovate; female disk small or absent.
      3. Fruit drupaceous; monoecious (in West Indies); disk present; staminodes often present ..... 5. **Cicca**
      3. Fruit pithy; dioecious; disk and staminodes absent. .... 6. **Aporosella**
   2. Fruit fleshy but at length dehiscent; calyx-lobes 6; leaves linear-oblong; female disk urceolate. ..... 7. **Emblica**

Sect. 4. **Ciccopsis** Webster, Contr. Gray Herb. 176: 57. 1955.

Shrubs or trees with phyllanthoid branching; cataphylls persistent; branchlets compressed, angled, often borne on spur-shoots; leaves with persistent stipules, corrugate petioles, chartaceous blades; monoecious, inflorescence semi-cauliflorous, the floriferous branchlets more or less fascicled on short spurs. Male flower: calyx-lobes 6, reflexed; disk-segments 6; stamens 3, free, the filaments erect; anthers deflexed at connective; pollen grains tricolporate, angular-aperturate. Female flower: calyx-lobes 6; disk 3-angled; ovary of 3 carpels; styles free, horizontal, bifid. Fruit and seeds unknown.

TYPE SPECIES: *Phyllanthus pseudocicca* Griseb.

This monotypic section is represented only by the type species, which is endemic to a relatively small area in eastern Cuba. Its relationships are somewhat dubious at present because of the doubt as to the nature of the fruit. However, there is little doubt that it is fairly closely related to sect. *Cicca*, if indeed that group is not its nearest ally. The pollen grains of *Cicca* are rather similar, and its cauliflorous condition could be rather easily derived from the semi-cauliflorous behavior of *Ciccopsis*. On the other hand, various African species in subg. *Kirganelia* — in particular *P. physocarpus* Muell. Arg. — have a suggestive general resemblance to *P. pseudocicca* in both floral and vegetative morphology. It is quite possible that sect. *Ciccopsis*, when better understood, may prove to represent the closest approach to a connecting link between subg. *Kirganelia* and subg. *Cicca*.

Section *Ciccopsis* is of further phylogenetic interest because of its apparent relationship to sect. *Omphacodes* (subg. *Xylophylla*). Indeed *P. pseudocicca* and the type species of that section, *P. subcarnosus*, are so strikingly similar in leaf venation and details of floral morphology that a fairly close degree of affinity between them appears highly probable, even though they are widely separated in the linear arrangement of taxa. The somewhat fleshy fruit and the ecological requirements of *P. subcarnosus* further suggest a general relationship to subg. *Cicca*. In fact, if it were not

for their areolate pollen grains, the two species of sect. *Omphacodes* could just as well be put adjacent to sect. *Ciccopsis* in the present arrangement.

6. **Phyllanthus pseudocicca** Griseb. Goett. Nachr. **1865**(7): 166. 1865; Muell. Arg. in DC. Prodr. **15**(2): 384. 1866.
(PLATE XV, *figs. A–C*).

Diasperus pseudocicca (Griseb.) O. Ktze. Rev. Gen. **2**: 600. 1891.
Phyllanthus brevistipulus Urb. Symb. Ant. **9**: 183. 1924.
Phyllanthus punctulatus Urb. ibid. 184.

A glabrous shrub (Ekman) or slender tree to c. 10 m. high (Wright); branches of previous year 3 — 4 mm. thick, with smooth or furrowed greyish bark, old nodes with spur-shoots c. 0.5 — 2 cm. long, 1.5 — 2 mm. thick, smooth or in age roughened with the cataphyll bases. Cataphylls dark brown, indurate, persistent, not reflexed: stipules broadly triangular, c. 1 mm. long and broad, blunt, typically entire, fused at the base into a massive scale; blades lanceolate, inconspicuous, c. 0.5 mm. long or less. Branchlets in part scattered along branches of current year, in part clustered on spur-like branches from the axils of nodes on old wood (i.e., on branches of previous years), 3 — 10 cm. long, 0.5 — 1 mm. thick, somewhat compressed, angled, stramineous, slightly shiny, with 5 — 9 leaves; first internode (5–) 10 — 17 mm. long, median internodes (5–) 7 — 10 (–15) mm. long. Leaves: stipules appressed, persistent, triangular, 0.5 — 1 mm. long and about as broad, blunt-tipped, dark reddish-brown, entire. Petiole (2.5–) 3 — 4 mm. long, stramineous, flattened adaxially, transversely corrugate-lamellate. Leaf blades chartaceous, plane, elliptic or ovate, 2.5 — 5 (–6.5) cm. long, 1.5 — 3 (–4) cm. broad, obtuse or rounded at the tip, mostly obtuse at the base; above olivaceous or brownish (when dried), somewhat shiny, midrib plane or incised, laterals slightly raised, subconspicuous; beneath greyish-green (puncticulate with whitish waxy atoms) or yellowish, the midrib and laterals (4 or 5 on a side) conspicuously raised, anastomosing to form a prominent reticulum; margins thickened, plane or reflexed.

Monoecious (rarely dioecious?); floriferous branchlets sometimes nearly or quite aphyllous (the leaves reduced to cataphylls) but usually with only the proximal 2 — 4 leaves reduced and subtending male cymules, the distal leaves typical and subtending bisexual cymules of one female and several male flowers; occasional branchlets producing only male flowers.

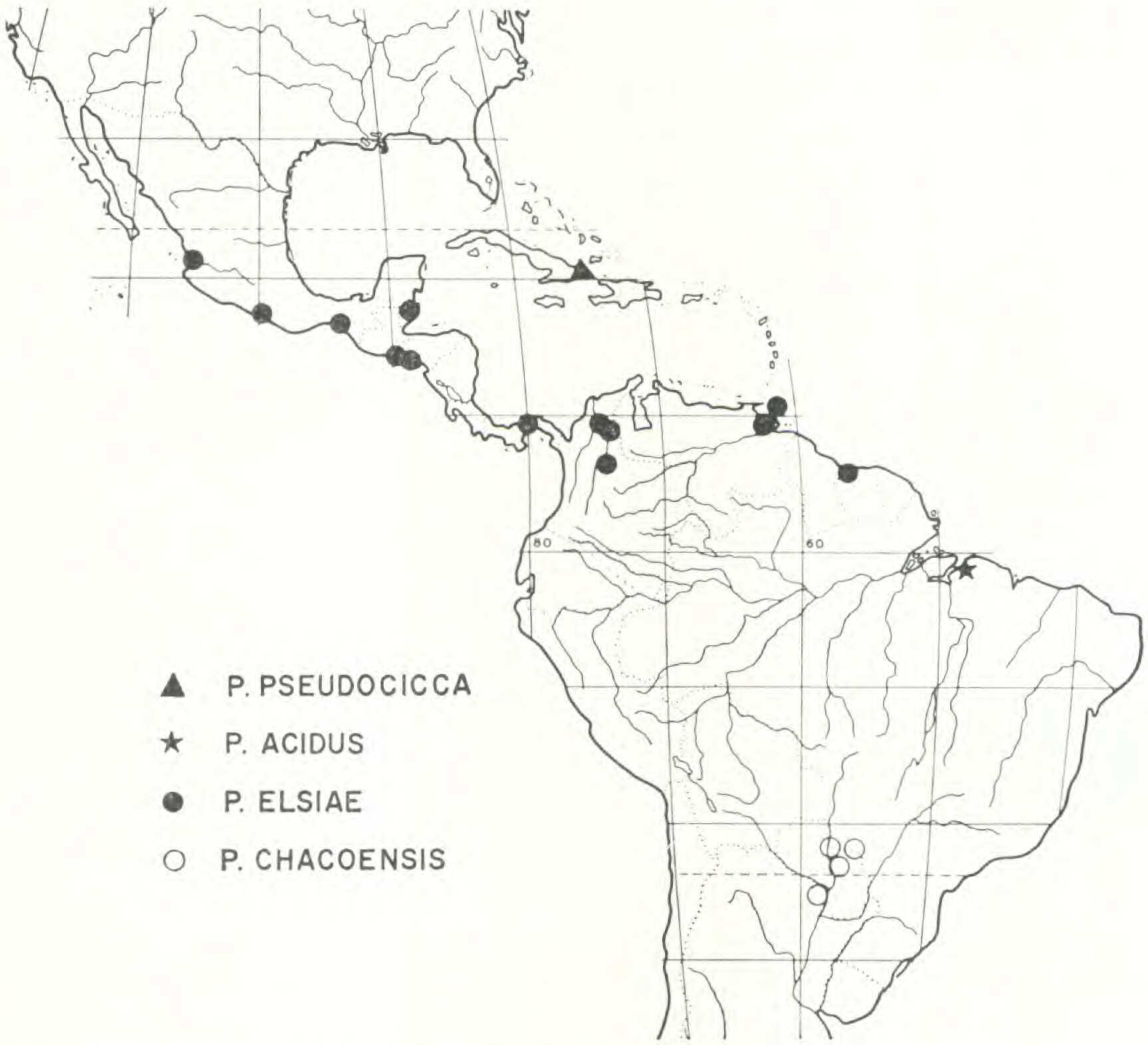
Male flower: pedicel c. 2 mm. long, stramineous, smooth, definitely enlarged above the middle, the enlarged portion often with a few reddish-brown cells. Calyx-lobes 6, biseriate, subequal, bent and reflexed or flaring from above the middle at anthesis, oblong-obovate, c. 0.75 — 0.9 mm. long, 0.45 — 0.6 mm. broad, rounded at the tip, entire, the midrib unbranched, the midrib area somewhat thickened and fleshy, the margins thin, scarious, subhyaline. Disk-segments 6, erect and substipitate, quadrate, c. 0.2 mm. in diameter, crenulate, pitted. Stamens 3, free except at

the very base (rarely 2 of them united), the filaments terete, erect, 0.4 — 0.5 mm. long; anthers sharply deflexed at the connectives, strongly flattened dorsiventrally, c. 0.2 mm. long, 0.3 mm. broad; anther-sacs strongly divergent, convergent at the apex but the slits not confluent; pollen grains tricolporate, c. 18 μ in diameter, angular-aperturate, the colpi narrowly bordered, not quite confluent at the poles.

Female flower: pedicel c. 10 mm. long, somewhat thickened distally. Calyx-lobes 6, subequal, oblong, c. 0.6 — 0.8 mm. long, 0.4 — 0.5 mm. broad, obtuse or acute, entire, somewhat spreading but not flaring as in the male, rather thicker and fleshier than the male, the scarious margin not so pronounced. Disk 3-angled, as of 6 segments fused in pairs, flat, thin, entire, not pitted. Ovary depressed-globose, sessile, smooth, trigonous, 6-sulcate; styles free, horizontally appressed to the ovary, 0.35 — 0.4 mm. long, bifid or $\frac{1}{3}$-parted, the branches divergent or divaricate, the blunt tips spreading or slightly recurved.

Mature fruit and seeds not examined (ex Alain, a capsule 3 — 4 mm. in diameter).

Collected in flower in June and July.



MAP III. Distribution of the American species of subg. *Cicca*.

TYPE: Cuba, Oriente, Cuchillas de Baracoa, a slender tree about 40 ft. high, flowers whitish, June 21, *Wright 1940* (GOET, holotype; G, GH, MO, isotypes; data ex GH).

DISTRIBUTION: endemic to the mountains of the Sagua-Baracoa range, Oriente Province, Cuba (Map III).

CUBA. ORIENTE: Sierra de Nipe, prope Rio Piedra, 4 Oct. 1919, *Ekman 9825* (S, HOLOTYPE of *P. punctulatus*); Moa region, Mina Cromita, Cayoguan, west of Punta Gorda, 24 July 1944, *Clemente & Alain 4079* (MICH); pineland barrens, Charrascos de Pena Prieta, Toa, alt. 600 m., 30 July 1953, *Alain 3484* (GH); same locality, 30 Dec. 1953, *Alain 3662* (GH); Baracoa, in the valley of the Rio Macaguanigua, 19 Jan. 1915, *Ekman 4323* (S, ISOTYPE of *P. brevistipulus*); Cuchillas de Baracoa, *Wright 1940* (G, GH, GOET, MO).

This extremely interesting species, although a phylogenetic relict and apparently rather rare, is not geographically narrowly confined, since its known range in the Sagua-Baracoa massif of Oriente Province is about 100 miles east to west. Its ecological requirements are not well known, the habit of pineland barrens as recorded by Alain being our only sure information. Judging from the data of Alain and others, however, it is evident that *P. pseudocicca* definitely does not occupy swamp woods or sublittoral forest habitats as do its relatives *P. acidus* and *P. elsiae*.

It is especially unfortunate that no mature fruits have been available for examination, since fruit structure is particularly significant in assessing relationships in subg. *Cicca*. The statement by Alain (Flora de Cuba 3: 53. 1953) that the fruit is a "capsula de 3 — 4 mm." may well be correct, for the ovary wall in *P. pseudocicca* at anthesis does not appear to be as thick as it is in *P. acidus;* however, the dehiscence of the fruit of *P. pseudocicca* may still not be typical for the genus. The lack of available fruits for examination is perhaps related to some peculiarity in the flowering habits of the species. Of the seven collections examined, five were completely sterile, and one of these, *Alain 3484*, was made only six days later in the year than the copiously fertile collection *Clemente & Alain 4079*.

The two species proposed by Urban, *P. brevistipulus* and *P. punctulatus*, were both founded on sterile Ekman collections. Urban compared the former to *P. nutans*, a completely different plant, and apparently was unaware that Grisebach had proposed the name *P. pseudocicca* for the same plant. Alain (loc. cit.) has already reduced *P. brevistipulus* to synonymy, and I feel certain that *P. punctulatus* merits the same treatment Urban merely compared its habit to that of *P. discolor* and *P. nutans* and added "sine dubio longe diversus." His comment was correct as far as it went, for the plant in question is indeed quite different from those two species. But Urban failed to realize that the type specimen of his *P. punctulatus* merely represents a large-leaved form of *P. pseudocicca*. The pale, slender branchlets c. 1 mm. thick, which indicate that the Ekman specimen belongs to *P. pseudocicca*, incidentally serve to distinguish this

species from another vegetatively similar Oriente species, *P. leonis*, which is often found in the sterile condition. In *P. leonis* the branchlets are mostly 1.5 — 2 mm. thick and are definitely angled.

Sect. 5. **Cicca** (L.) Muell. Arg. Linnaea **32**: 50. 1863; emend.

Cicca L. Mant. 124. 1767.
Tricarium Lour. Fl. Cochin. 557. 1790.
Staurothylax Griff. Notul. **4**: 476. 1854.
Phyllanthus sect. *Cicca* subsect. *Eucicca* Muell. Arg. loc. cit.; DC. Prodr. **15**(2): 413. 1866.
Phyllanthus sect. *Typophyllanthus* subsect. *Cheramela* O. Ktze. Lex. Gen. Phaner. 434. 1904.

Trees with phyllanthoid branching, the flowers more or less cauliflorous. Monoecious or rarely dioecious. Male flower: calyx-lobes 4; disk of 4 segments; stamens mostly 4, filaments free, anthers dehiscing vertically; pollen grains globose, tricolporate, the colpi meeting at the poles. Female flower: calyx-lobes 4; disk lobed or separated into 4 segments; staminodes often present; carpels 3 or 4; styles free except at base, deeply bifid, spreading. Fruit drupaceous, endocarp bony; seeds 1 or less commonly 2 per fertile locule.

TYPE SPECIES: *Phyllanthus acidus* (L.) Skeels

The single species which comprises this monotypic section is so closely related to the representatives of sect. *Aporosella* that — despite the strong morphological discontinuity — it could almost as logically be associated with them in a single section. The production of staminodes in the female flower and the truly drupaceous nature of the fruit are the strongest distinguishing characters of sect. *Cicca*.

Robinson (Phil. Jour. Sci. Bot. **4**: 87. 1909; **6**: 323. 1911) has advocated generic status for *Cicca*, largely on the basis of the fruit, and has been followed by Merrill and other workers. There is of course no doubt that *Cicca* is a distinctive group, so that the question of its generic vs. infrageneric rank is to some extent a matter of judgment. In my opinion its close alliance with sects. *Ciccopsis* and *Aporosella* makes the inclusion of *Cicca* within *Phyllanthus* the most logical treatment.

It should be noted that the circumscription of sect. *Cicca* is here drastically altered from Mueller's concept so as to include only his subsect. *Eucicca* and to exclude his subsects. *Margaritaria*, *Prosorus*, and *Ciccoides*. Mueller's erroneous description of the fruit of *P. acidus* as capsular suggests that he had seen no good fruiting specimens and was extrapolating from the more or less dehiscent fruit of the other subsections. These latter, however, differ from *P. acidus* not only in their fruits but also in their non-phyllanthoid branching, annular floral disk, and fleshy seed-coat; indeed they scarcely have more in common with *P. acidus* than superficially rather similar tetramerous flowers. The species in these three subsections

should all be removed from *Phyllanthus* and placed together in the genus *Margaritaria*.

The following West Indian species which have been included in *Phyllanthus* sect. *Cicca* are therefore to be transferred from the genus:

1. *Phyllanthus nobilis* (L.f.) Muell. Arg. = *Margaritaria nobilis* L. f.

2. *Phyllanthus virens* (Griseb.) Muell. Arg. = **Margaritaria tetracocca** (Baill.) comb. nov. (*Wurtzia tetracocca* Baill. Adansonia **1**: 187. 1860–61).

3. *Phyllanthus scandens* (Wr. ex Griseb.) Muell. Arg. = **Margaritaria scandens** Wr. ex Griseb.) comb. nov. (*Cicca scandens* Wr. ex Griseb. Goett. Nachr. **1865**: 165–166. 1865).

4. *Phyllanthus hotteanus* Urb. & Ekm. (Ark. Bot. [Stockholm] **22A**[8]: 61. 1929) = **Margaritaria hotteana** (Urb. & Ekm.) comb. nov.

7. **Phyllanthus acidus** (L.) Skeels, U.S.D.A. Bur. Pl. Ind. Bull. **148**: 17. 1909. (PLATE XV, *figs. D–F*).

Neli-pouli Rheede, Hort. Malabar. **3**: 57, *pls. 47, 48*. 1682.
Malus indica, fructu parvo rotundo acido striato Burm. Thes. Zeyl. 148. 1737.
Averrhoa ramis nudis fructificantibus, pomis subrotundis L. Fl. Zeyl. 80. 1747.
Cheramela Rumph. Herb. Amb. **7**: 34, *pl. 17, fig. 2*. 1750.
Averrhoa acida L. Sp. Pl. 428. 1753.
Cicca disticha L. Mant. **1**: 124. 1767.
Cicca nodiflora Lam. Encycl. **2**: 1. 1786.
Cicca racemosa Lour. Fl. Cochin. 556. 1790.
Phyllanthus longifolius Jacq. Hort. Schoenbr. **2**: 36, *pl. 194*. 1797.
Cicca acidissima Blanco, Fl. Filip. ed. 1, 700. 1837.
Phyllanthus cicca Muell. Arg. Linnaea **32**: 50. 1863.
Phyllanthus cicca β bracteosus Muell. Arg. ibid.
Phyllanthus distichus (L.) Muell. Arg. in DC. Prodr. **15**(2): 413. 1866.
Phyllanthus distichus f. *nodiflorus* (Lam.) Muell. Arg. op. cit. 414.
Phyllanthus acidissimus (Blanco) Muell. Arg. op. cit. 417.
Diasperus distichus (L.) O. Ktze. Rev. Gen. **2**: 599. 1891.
Cicca acida (L.) Merr. Interpr. Rumph. Herb. 17. 1917.

A small or medium-sized glabrous tree up to 10 m. high, with rough grey bark; older branches subterete, up to c. 1.5 cm. thick, greyish brown, with rather prominent lenticels; terminal branches of current year dark brown, smooth, remaining spur-like or elongating up to c. 8 cm., 3 — 5 mm. thick, producing usually seven or eight leafy branchlets; inflorescences mostly borne on lateral spur-shoots (less than 1 cm. long) on older wood. Cataphylls blackish brown, rather firm but breaking away and not persisting, the stipules triangular-ovate, c. 1.5 mm. long, with entire to fimbriate margins; blade similar but narrower, acuminate, up to 2 mm. long. Deciduous branchlets ascending, (20–) 25 — 52 cm. long, c. 1.5 — 3 mm. thick, pale brown, terete (somewhat flattened or subangled toward apex), smooth, with 25 — 40 leaves; first internode 1 — 5 cm. long, median internodes c. 0.5 — 1 cm. long. Leaves: stipules appressed, the bases more

or less persistent, triangular-acuminate, c. 0.8 — 1.2 mm. long and (0.3–) 0.5 — 0.8 mm. broad (the proximal ones somewhat larger), not auriculate, dark brown, scarious, entire or denticulate-fimbriate. Petiole 2.5 — 4 mm. long, yellowish brown, more or less rugose, with two blunt ridges and a low median ridge on the adaxial side. Leaf blade chartaceous, broadly ovate to ovate-lanceolate, (4–) 5 — 9 cm. long, (2–) 2.5 — 4.5 cm. broad, acute (sometimes abruptly so) at the tip, obtuse or rounded at the base; above olivaceous, sublucid, the proximally impressed midrib running to the tip, laterals ascending, reticulum of tertiary branches evident to conspicuous; beneath pale greyish brown, the midrib prominently raised, the laterals (c. 5 — 7 on a side) ascending, raised, anastomosing within the margins, forming with the tertiaries a fine subprominent slightly raised reticulum; margins undifferentiated, plane.

Monoecious (in West Indian material); flowers borne in dense pulviniform cymules at the nodes of "naked" branchlets on older wood, and usually also on the proximal branchlets of the current year's growth (at the tip of the branch). Cymules of cauline inflorescence axes (which are merely modified deciduous branchlets) bisexual, each with 1 — 9 female flowers accompanied by c. 25 — 40 males. First branchlets of the current year's growth often bearing bisexual cymules with 1 — 2 female flowers and a dozen (or less) males; succeeding ones with male cymules; distalmost branchlets quite sterile (sometimes no branchlets with bisexual cymules, or occasionally all branchlets sterile). Bracts of cymules blackish brown with reddish brown scarious fimbriate margins, less than 1 mm. long.

Male flower: pedicel slender, c. 1.5 — 3 mm. long. Calyx-lobes 4, subequal (the inner pair rather broader), elliptic to suborbicular, 1.1 — 1.4 (–1.5) mm. long, 0.8 — 1.3 (–1.4) mm. broad, rounded or obtuse at the tip, entire, the midrib unbranched. Disk-segments 4, more or less orbicular, c. 0.2 — 0.3 mm. across, not massive, entire. Stamens 4 (rarely 3), filaments free (at most slightly coherent at base), slender (c. 0.1 mm. thick), erect, 0.4 — 0.5 (–0.6) mm. long; anthers more or less deflexed at the connectives, emarginate or occasionally minutely apiculate, broadly elliptic to suborbicular, c. 0.25 — 0.3 mm. long, 0.3 — 0.35 mm. broad; anther-sacs parallel, dehiscing longitudinally, the slits not confluent; pollen grains 16 — 19 μ in diameter, tricolporate, not angular-aperturate, the colpi conspicuously bordered, confluent at the poles.

Female flower: pedicel straight, terete and rather stout (in fresh material; often becoming wrinkled or sharply ridged on drying), increasing in length from c. 1.2 — 1.5 mm. at anthesis up to c. 2.3 — 5 (–6) mm. in fruit, c. 0.3 — 0.5 mm. thick. Calyx-lobes 4, at first erect, later spreading, subequal, triangular-ovate or elliptic, (1–) 1.2 — 1.4 mm. long, (0.9–) 1 — 1.25 mm. broad, obtuse or rounded at the tip, thickened at the base, entire, the midrib unbranched. Disk c. 1 — 1.2 mm. across, mostly deeply lobed or separated into 4 quadrate or reniform segments, these c. 0.2 — 0.3 mm. across. Ovary at first more or less pyriform, c. 0.8 — 1.1 mm. high, 0.8 — 1.2 mm. in diameter, smooth, brownish, shallowly 3- or 4-lobed, usually definitely stipitate, the broad gynophore c. 0.2 — 0.25 mm. high;

styles very shortly connate into a column 0.2 — 0.25 mm. high, recurving, deeply bifid to the column, the slender tapering branches c. 0.8 — 1 mm. long. Staminodia 0, 1, or 2 (rarely to 4, ex Mueller) per flower, resembling the stamens but filaments much shorter.

Fruit drupaceous, oblate, of 3 or less commonly 4 carpels shallowly 6- or 8-lobed, the flesh (exocarp) firm, greenish yellow to creamy white, acid in taste, quite variable in size: when fresh, c. 1 — 1.5 cm. high, (1.2–) 1.5 — 2 (–2.5) cm. in diameter. Endocarp very hard and bony, the carpels firmly united and never separating on drying of the fruit, subglobose or oblate, deeply but obtusely ridged, c. (4.8–) 5 — 7 (–9) mm. high and 6 — 9 (–16.5) mm. in diameter. All carpels of a fruit rarely fertile, usually only 1 or 2 (–3) cells each developing 1 or less commonly 2 seeds. Seeds (when single) adaxially concave, c. 3.3 — 3.5 mm. long, 2.5 — 3 mm. broad; seed-coat thin (except around the hilum), brittle, light brown, smooth; hilum broad, circular, on the adaxial face.

Flowering (in the West Indies) mostly January through July; most flowering collections made January through March; sometimes flowering in the leafless condition, according to collectors.

TYPE: Linnaean Herbarium, sheet 592–3 (LINN). This specimen is here designated as the holotype, although ordinarily species first described by Linnaeus in the "Flora Zeylanica" would be based on specimens in the Hermann Herbarium (BM). As pointed out, however, by Trimen (Handb. Fl. Ceylon 4: 26. 1898), there is no specimen of the plant in Hermann's herbarium, and the drawing cannot be identified with certainty. Rheede's figures are good (except that the leaves are shown as opposite!), and following the strictest priority one could make one of his two plates the type; but in view of the doubt connected with Linnaeus's original treatment, it seems preferable to typify the basionym *Averrhoa acida* by a particular specimen.

DISTRIBUTION: native probably to South America (MAP III); cultivated on all of the larger islands of the West Indies. Only representative specimens are cited.

BAHAMAS: Andros, Fresh Creek, *J. I. & A. R. Northrop 653* (F). CUBA: Las Villas, La Sierra, *Jack 7851* (A, S, US). JAMAICA: *R. C. Alexander* (GOET). PUERTO RICO: Isabon, *Sintenis 6487* (F, G). ST. CROIX: Bassin, *A. E. Ricksecker 268* (F, US). ST. THOMAS: Canaan, *Eggers 372* (G, M). ANTIGUA: *Wullschlaegel 496* (GOET). GUADELOUPE: Basse-Terre, *Duss 2929* (US). MARTINIQUE: *Duss 955* (US). ST. VINCENT: *Caley* (G, W). ISLA DE PROVIDENCIA: *Proctor 3462* (US).

Carl Linné the younger was the first to observe that *Averrhoa acida* and *Cicca disticha* were synonymous (Suppl. Pl. 416. 1781); and he also questioned the distinctiveness of *Cicca* as a genus distinct from *Phyllanthus*. The rather variable inflorescence in this species, together with the confusion introduced by Linnaeus when he redescribed it (twenty years after the "Flora Zeylanica") as *Cicca disticha*, has resulted in a rather

complicated synonymy for the plant. Lamarck's *Cicca nodiflora* was based on a specimen in which the flowers were borne on leafy branchlets rather than on naked axes on older wood; but since both conditions may normally occur on the same plant, his name does not merit retention for a taxon of any rank. Jacquin's magnificent folded colored plate in the "Hortus Schoenbrunnensis" is the best illustration yet published of this species, and clearly shows both the hermaphrodite and unisexual flower forms.

The female flowers of *P. acidus* are unique in the presence of staminodes which at times apparently act as functional stamens. The number of staminodes per flower, however, is variable even in the same inflorescence and fluctuates on the same plant from 0 to 4. No flowering herbarium specimens were seen in which there was not at least one staminode in some of the flowers. Consequently, this feature could be used in support of the claim of *Cicca* to generic status; but the evidently close relationship of the present species to the two following more than outweighs the staminodial character, which after all appears to be a sort of "teratological" reversion and not a primitive character.

The number of fertile sporophylls is variable in both the male and female flowers of *P. acidus*. However, whereas there are regularly 4-carpelled flowers mixed among the predominantly 3-carpelled ones, fluctuations in the number of stamens are less common. Some trees appear to produce regularly male flowers with four stamens, while in others (represented by the herbarium specimens *Karsten s.n.* from Merida, Venezuela (W), and *Schwanecke 12* from Puerto Rico (W)), all flowers have only two or three stamens. In the *Schwanecke* collection, there are furthermore many flowers in which a pistillode-like structure occurs. However, it appears that this "pistillode" is actually a modified stamen, for in *P. acidus* it has not been observed in normal flowers with four stamens. It might be thought that these floral irregularities in *P. acidus* are related to its cultivated state; but if one may judge from the numerical fluctuations of the floral parts of *P. elsiae*, it seems more likely that there is simply an inherent tendency toward meristic variation in the flowers of *P. acidus*.

Phylogenetically, *P. acidus* is of great interest in that it forms a connecting link between sect. *Ciccopsis* and sect. *Aporosella*. Its androecium of stamens with elongated filaments and reflexed anthers, and its well-developed floral disk, agree with sect. *Ciccopsis;* but its massive ovary developing into an indehiscent fruit, its cauliflorous inflorescence, and its leaf form are more like sect. *Aporosella*. Sect. *Cicca* further agrees with sect. *Aporosella* in its tendency toward dioeciousness; although all West Indian specimens examined are monoecious, those from the Philippines are dioecious, as pointed out by Robinson (Phil. Jour. Sci. Bot. **4**: 87. 1909). On the other hand, its pollen grains appear to be somewhat less specialized than those of either *Ciccopsis* or *Aporosella*. If we conceive of the four American species of subg. *Cicca* as relict populations surviving from an anciently widespread ancestor, these cross-relationships and differential evolutions of organs can be mostly clearly and easily explained.

Heretofore, the relationships between *P. acidus* and the other American representatives of subg. *Cicca* have not been recognized, partly because of taxonomic confusion but perhaps mostly because of the prevalent misconception of the indigenous range of *P. acidus*. In common with many widely cultivated tropical plants, *P. acidus* has been regarded as of rather uncertain nativity. Nevertheless, all authors have credited the species to the Old World, and indeed most commonly to Madagascar and the Malay Islands. Trimen (Handb. Fl. Ceylon 4: 26. 1898), for instance, observes that it is "much grown in native gardens for its acid fruit . . . and no doubt an ancient cultivation." It is recorded by Merrill (Enum. Phil. Fl. Pl. 2: 397. 1923) as "of prehistoric introduction from Malaya." Numerous other authors could be cited in support of the "Malayan" origin of the plant, but on the other hand, there are some significant disclaimers. Thus Ridley (Fl. Malay Pen. 3: 216. 1924) cites it only from gardens, and Burkill (Dict. Econ. Prod. Malay Pen. 1: 537. 1935) classifies it as of "uncertain origin." J. J. Smith (Add. Fl. Arb. Jav. 12: 82–83. 1910), a usually careful observer, notes that the species, to the best of his knowledge, has never been encountered wild in Java, although it is much cultivated there. Leandri (Not. Syst. 7: 186. 1939) found no specimens of the species (even of cultivated trees) from Madagascar. The final impression given by a perusal of the literature is thus that of a "probably Malayan" plant which has never been discovered wild there!

In view of this nearly universal ascription of the homeland of *P. acidus* to the Indonesian region, it was a distinct surprise to find in the course of the present study that the closest congeners of the species are the two representatives of the New World sect. *Aporosella*, while on the other hand it has no close relatives in the Old World. In fact, specimens of *P. elsiae* have so often been misidentified as *P. acidus* that it is quite impossible to determine from published reports whether or not *P. acidus* is growing wild at a specific locality. Thus far attempts to discover the native habitat of *P. acidus* have been largely unsuccessful. The collections of Martius from Minas Geraes, cited by Mueller (Fl. Brasil. 11[2]: 68. 1873), have unfortunately not been examined; but another collection from the same state (*Wawra & Maly* [W]) appears definitely to represent a cultivated plant, as do two collections made by Karsten at Merida, Venezuela, and Bucaramanga, Colombia (both at W). Only one herbarium specimen has been examined which would appear to represent *P. acidus* in its native habitat; it was collected by Poeppig in 1832 on the island of Colares in the Pará River delta, northeastern Brazil (W). Poeppig's notation that the habitat of the plant was in littoral woods ("sylvis littoreis") suggests very strongly that he was dealing with the native plant; for one would expect that *P. acidus* might have ecological requirements similar to those of *P. elsiae*.

A search through the floristic publications of Huber and Ducke on the Amazon delta region has failed to turn up any record of *P. acidus*, under its accepted or any synonymous name. This, however, would not appear to cast any doubt on the authenticity of the Poeppig collection. The coastal Amazonian region contains so many large stretches which because

of the uninviting and inaccessible nature of the terrain are little-known botanically, that the existence of *P. acidus* in considerable abundance there is by no means excluded. If it inhabits the infra-mangrove forest zone, which is relatively narrow, it may have gone undetected, just as *P. elsiae* was until the studies of Lindeman in Surinam.

It is at the very least a remarkable and interesting coincidence that there is a similar uncertainty as to the origin of the oxalidaceous mimic of *P. acidus*, *Averrhoa bilimbi* L. The superficial resemblance of the two species is so arresting that it is not surprising that Linnaeus was misled into classifying both of them as species of *Averrhoa*. The geographical problem with regard to *Averrhoa bilimbi* is made even more puzzling by the fact that there is an equal uncertainty regarding the origin of the only other species in the genus, *A. carambola*. All three of these similar plants, which Burman grouped together as species of "Malus indica" are cultivated at present in tropical gardens throughout much of America and Asia; but the two species of *Averrhoa* show a much greater tendency to become naturalized. Knuth (Pflanzenf. ed. 2, 19a: 39. 1931) has in fact ascribed the origin of the genus to *Averrhoa* to Malaysia on the basis of the report by Koorders (Exkursionsfl. Java 2: 413. 1912) that both species are found wild in Java.

Many authors have remarked that the species of *Averrhoa* are "obviously of ancient cultivation" in the Indian and Malaysian regions. However, in view of our sure knowledge of the rapid diffusion of corn throughout the Old World (cf. Mangelsdorf & Oliver, Bot. Mus. Leafl. Harvard Univ. 14: 263–291. 1951), the possibility of a post-Columbian introduction from the New World must be admitted for *Averrhoa* as well as for *P. acidus*. Trimen (Handb. Fl. Ceyl. 1: 200. 1893) has already suggested that the two averrhoas were originally introduced into Ceylon from the New World by the Portuguese, and Merrill (Chron. Bot. 14: 301. 1954) states positively that this was the case, though without adducing any specific evidence. The investigation of *Averrhoa* from the phytogeographic point of view is of especial interest since it appears to be the only genus of more than one species which is unknown in the indigenous state.

When all the evidence is considered, it appears that *P. acidus* certainly, and both species of *Averrhoa* probably, are indigenous to the New World and have been introduced into the Old World in post-Columbian times. Although the exact natural range of *P. acidus* is still unknown, it definitely is native to the Pará River delta, and will probably be discovered in a number of localities in the Amazon delta region. By analogy with the documented evidence for *P. acidus*, it appears most likely that both species of *Averrhoa* are also originally American plants which have had a similar history. The great superficial resemblance between these three species may not be entirely coincidence, for it is possible that all three are members of the sub-littoral forests of the South American coastline; and their similarity in life form may have a selective basis. Probably, as suggested by Merrill and Trimen, these plants were first encountered by the Portuguese on the Brazilian coast and from there carried to India and

other parts of the Old World. The fascinating problems in ethnobotany posed by such species as *P. acidus* cannot be resolved with certainty until a more thorough knowledge of the coastal flora of northeastern Brazil can be correlated with an analysis of the earliest Portuguese explorations there. When this is accomplished, a definitive evaluation can be made of the hypotheses presented here.

Sect. 6. **Aporosella** (Chodat) stat. nov.

Aporosella Chodat, Bull. Herb. Boiss. 2 ser. **5:** 488–489. 1905.

Trees with completely cauliflorous inflorescences, flowering with the appearance of the leaves. Dioecious; flowers in aphyllous thyrsi (the leaves reduced to bracts). Male flower: calyx-lobes usually 4; disk absent; stamens usually 4, filaments free, anthers dehiscing vertically; pollen grains globose, tricolporate. Female flower: calyx-lobes 4; disk absent; staminodes absent; carpels 2 or 3; styles connate at the base, bifid or lacerate. Fruit indehiscent and woody, the endocarp bony, with 2 or 3 cells; fertile locules 1 or 2 per fruit, seeds solitary.

TYPE SPECIES: *Phyllanthus chacoensis* Morong [*Aporosella hassleriana* Chodat].

This small section of two American species is so divergent from the great majority of the species of *Phyllanthus* that on the basis of morphological characters alone it could be maintained as a distinct genus. The combination of arboreal habit, dioecious completely cauliflorous inflorescence, woody indehiscent fruit, and absence of a floral disk is unique, and indeed defines the group much more sharply from the typical species of *Phyllanthus* than do the characters which distinguish such genera as *Glochidion*, *Sauropus*, and *Breynia*. However, there can be no doubt that the two species of *Aporosella* are closely related to *P. acidus*, and through that species, perhaps via *P. pseudocicca*, to more "typical" species of *Phyllanthus* in subgenus *Kirganelia*. It would thus be manifestly contrary to natural relationship to recognize *Aporosella* as a distinct genus and at the same time leave sects. *Cicca* and *Ciccopsis* within *Phyllanthus*. A segregate genus comprising sects. *Ciccopsis*, *Cicca*, and *Aporosella* would be more satisfactory except that it would be nearly impossible to distinguish it from *Phyllanthus*. Consequently, it does not appear practicable at the present time to recognize any part or all of subg. *Cicca* as an independent genus.

Pax and Hoffmann (Pflanzenr. IV. 147. XV: 105–107. 1922) seriously erred in placing *Aporosella* in the subtribe Antidesminae between *Aporosa* and *Antidesma*. The resemblance between these three genera is confined to a superficial similarity in inflorescence and fruit; but the phyllanthoid branching of *Aporosella* clearly precludes its belonging to the Antidesminae. The original ascription of the type species to *Phyllanthus* by Morong (Ann. N. Y. Acad. Sci. 7: 218. 1892) after all comes closest to the mark.

8. **Phyllanthus elsiae** Urb. Repert. Sp. Nov. **15**: 405–406. 1919. (PLATE XV, *figs. G–I*).

Glabrous small or medium-sized tree c. 7 — 15 m. high with a dense crown, the habit similar to that of *P. acidus;* older branches terete, c. 0.5 — 1.5 cm. broad, sometimes with conspicuous lenticels; branches of current year with up to 10 leafy branchlets. Cataphylls blackish brown, indurate, more or less deciduous; stipules triangular-ovate, c. 1.5 mm. long, with fimbriate margins; blade similar but narrower. Deciduous branchlets ascending, (10–) 15 — 30 cm. long, c. 1.3 — 1.8 mm. thick, pale to dark brown, obscurely angled or terete, smooth, with c. 10 — 20 leaves; first internode (0.3–) 1 — 2.5 (–4) cm. long, median internodes c. 1 — 1.5 cm. long. Leaves: stipules appressed, triangular-lanceolate, c. 0.8 — 1.2 mm. long, 0.5 — 0.7 mm. broad, acute, blackish-brown, scarious, subentire, not auriculate at the base. Petiole 2.5 — 3.5 mm. long, subterete, often corrugated, the edges of the blade decurrent on the adaxial face as two straight rather inconspicuous flanges. Leaf-blade chartaceous (sometimes stiffly so) mostly broadly elliptic to suborbicular and rather abruptly contracted to a short acumen, mostly 3 — 5 (–7) cm. long, 2 — 4 (–5) cm. broad, obtuse or rounded at the base; above olivaceous to plumbeous, the proximally impressed midrib running to the tip, laterals ascending, reticulum of tertiary veinlets obscure to subprominent; beneath greenish or greyish to reddish brown, the midrib prominently raised, the laterals (usually 4 or 5 on a side) ascending, raised, anastomosing within the margins, forming with the tertiaries a fine subprominent slightly raised reticulum; margins plane or often more or less undulate or crisp.

Dioecious; flowers borne only on naked branchlets (thyrsi) on older wood of the stem (these clustered on spur-shoots in the axils of old leaf-scars), never on leafy branchlets of the current year's growth. Bracts indurate, blackish brown; stipules broadly triangular, umbonate, margins lacerate-fimbriate, c. 1 — 1.5 mm. long and 1.2 — 1.4 mm. broad, the blade c. 0.7 — 1.5 mm. long. Male inflorescence axes (1–) 1.5 — 7 cm. long, with 5 — 13 (–19) nodes; cymules with c. 10 — 20 flowers. Female inflorescence axes (2–) 3 — 6 (–9) cm. long, with 7 — 13 (–19) nodes; cymules with 1 — 3 (rarely 4) flowers.

Male flower: pedicel (1.2–) 1.5 — 3 (–5) mm. long. Calyx-lobes 4, subequal, obovate, 1 — 1.7 mm. long, 0.7 — 1 mm. broad, obtuse or rounded at the tip, entire to minutely fimbriate, the hyaline margins narrow to rather broad, midrib unbranched. Disk absent. Stamens 4 (rarely 3 or 5); filaments free, slender, erect, only 0.1 — 0.25 mm. long; anther-sacs parallel, dehiscing vertically, the slits not confluent; pollen grains 17–21 μ in diameter, slightly angular-aperturate, colpi very narrow and not meeting at the poles.

Female flower: pedicel terete or subangular, straight or curved, smooth, (1–) 1.5 — 2 (–3) mm. long. Calyx-lobes 4, subequal (the outer somewhat smaller), obovate or oblong, 0.8 — 1.3 mm. long, (0.4–) 0.6 — 0.8 mm. broad, rounded at the tip, subentire to minutely fimbriate, the midrib

unbranched. Disk absent. Ovary ovoid, c. 0.8 — 1.2 mm. in diameter at anthesis, rugulose, not stipitate, of 3 or rarely 2 carpels; styles connate at the base into a column c. 0.3 — 0.5 mm. high, bifid to the column, the flattened acute tapering tips spreading or ascending, 1.8 — 2.3 mm. long. Staminodia absent.

Fruit mostly oblate spheroidal, 3-celled (rarely 2-celled), (5–) 6 — 8.5 mm. high, (5.5–) 6 — 8.5 (–10.5) mm. broad, obtusely lobed, indehiscent, dry and woody, the outer layer soft and pithy, the inner hard and bony. Fertile carpels usually 1 or 2 per fruit, each with a single seed. Seeds flattened, smooth, the brittle testa pale brown or stramineous, c. 3 — 3.5 (–4) mm. long, (2–) 2.2 — 2.4 (–2.7) mm. broad; hilum conspicuous, c. 0.7 — 1 mm. across, dark reddish-brown, triangular or roundish.

Collected in flower January through March; in fruit April through December.

TYPE: Tobago, Auchenskeoch Beach, March 25, 1914, *W. E. Broadway 4789* (US 759650; LECTOTYPE). The specimen in the U. S. National Herbarium is here designated as the lectotype, as it is the only sheet seen of the type collection; the original specimen in Urban's herbarium at Berlin-Dahlem presumably was destroyed during World War II.

DISTRIBUTION: low forests along lagoons and rivers, usually near sea-level, northern South America to southern Mexico (MAP III).

TOBAGO: Auchenskeoch Beach, *Broadway 4789* (US, LECTOTYPE), *5910* (MO); Studley Park, near the sea, *Broadway 4557* (F, GH, MO, US). TRINIDAD: Erin, sea shore, *Broadway 7845* (MO, S), *9112* (A, MO); Rousillac Swamp, *Swabey* (TRIN 12558).

Because of the variability and interesting distribution of this species, the following representative specimens are cited from throughout its range.

MEXICO: NAYARIT: Mexcatitlan, nearly at sea level, shallow lagoons, growing in water, *Mexia 1005* (A, US); same locality, *Ortega 5545* (US). GUERRERO: near sea beach, Acapulco, *Palmer 595* (A, US). CHIAPAS: Paredon, Tonala, *Matuda 16274* (US).

BRITISH HONDURAS: Belize River, *Record B.H.52* (US).

EL SALVADOR: SANTA ANA: El Desagüe, Laguna de Quija, alt. 440 m., *Pittier 1902* (US). SAN MIGUEL: Laguna de Olomega, alt. c. 75 m., *Standley 20983* (GH). SONSONATE: Izalco, in park, *Standley 22234* (GH).

PANAMA: CANAL ZONE: banks of Chagres River, below Gatun, near sea-level, *Maxon 4797* (US); forest along the Rio Indio de Gatun, near sea-level, *Pittier 2776* (US).

COLOMBIA: BOLIVAR: San Martin de Loba, *Curran 409* (GH); river-marsh, Magangue, *Pennell 3954* (US). SANTANDER: Puerto Wilches, *Daniel 1178* (US).

VENEZUELA: DELTA: Rio Manimo, Buelta Triste, *Bond, Gillin, & Brown 158* (GH, US), *163* (GH).

BRITISH GUIANA: Botanic Gardens, Georgetown, *Archer 2576* (US).

SURINAM: swamp, Nickerie, Nanni-creek, near Kaaimancreek, common, *Geyskes 154* (A).

The broad distribution of *P. elsiae*, which is probably locally common in numbers of mainland littoral areas along the Caribbean, has not been recognized heretofore because of the confusion between it and *P. acidus*. Since the original publication of the species by Urban, all of the collections cited above with the exception of that of Swabey have either been mistaken for *P. acidus* or left unnamed. Lanjouw and Lindeman, however, have independently come to the conclusion that the tree of the Surinam swamps discussed by Lindeman (Veg. Coastal Reg. Suriname, Table II. 1953) under the name *P. acidus* actually represents a different species (personal communication).

The habitat of *P. elsiae*, as reported by Lindeman, is the swamp woods or moist forest which often occurs near the coastline directly behind the mangrove belt, and only a few feet above sea-level. Only the collection made in El Salvador by Pittier records the species at an elevation of greater than 100 meters. It is probable that further collecting will show the range of *P. elsiae* to be almost continuous along the coast from Surinam to British Honduras and, on the Pacific side, from Panama to Mexico. As far as can be determined, however, the species does not occur along the Pacific Coast of South America.

The resemblance between *P. acidus* and *P. elsiae* is so close that the past confusion is quite understandable. Both plants are cauliflorous trees with tetramerous flowers and similar indehiscent fruits. However, the differences between the two species are so important that they seem best assigned to separate sections. In contrast to the West Indian representatives of *P. acidus*, which are monoecious, with a well-developed floral disk and drupaceous fruit, *P. elsiae* is dioecious, with no floral disk and with a woody rather than fleshy fruit. Even sterile specimens of the two species are readily separable, *P. acidus* having branchlets with 25—40 leaves and ovate leaves gradually narrowed to the tip, while *P. elsiae* has branchlets with 10—20 leaves and more rotund leaves which are usually abruptly narrowed at the tip. Furthermore, *P. elsiae* is always perfectly cauliflorous (the leafy branchlets invariably being sterile), while *P. acidus* usually has flowers produced on the leafy branchlets as well as the aphyllous thyrses.

Much more closely related than *P. acidus* is the type species of *Aporosella*, *P. chacoensis*. This plant, native to the Chaco region of Argentina and Paraguay, resembles *P. elsiae* so closely that one might almost consider the two taxa as subspecies of a single species. However, the fruits of *P. chacoensis* are always 2-celled, and although this character is not invariable in distinguishing it from *P. elsiae* (which rarely has a few 2-celled fruits in addition to the usual 3-celled ones), the styles furnish an adequate diagnostic feature. They are much broader and shorter (less than 1 mm. long) in *P. chacoensis* than in *P. elsiae*. It appears best, therefore, to consider the plants in question as two closely related but distinct species.

Sect. 7. **Emblica** (Gaertn.) Baill. Etud. Gen. Euphorb. 626. 1858.

Emblica Gaertn. Fruct. **2**: 122–123, *pl. 108, fig. 2.* 1790.
Dichelactina Hance in Walp. Ann. **3**: 375. 1852–53.

Trees with phyllanthoid branching; branchlets often fascicled at the nodes; leaves oblong to linear, closely distichous. Monoecious; flowers in axillary cymules at the proximal nodes of branchlets. Male flower: calyx-lobes usually 6; disk of 6 small segments, or absent; stamens normally 3, filaments united into a column; anthers sessile atop the column, dehiscing vertically; pollen grains subglobose to subprolate, 4- or 5-colporate. Female flower: pedicel very short; calyx-lobes 6; disk a lacerate cup enveloping the ovary; ovary smooth, of 3 carpels; styles shortly connate, twice bifid, distally dilated. Capsule with a fleshy exocarp, the cocci rather thick and massive, eventually separating from a well-developed columella. Seeds 2 in each locule, trigonous, somewhat unequal.

TYPE SPECIES: *Emblica officinalis* Gaertn. loc. cit. (= *Phyllanthus emblica* L.).

This section of a few Old World species is here given the same circumscription as that of Hooker (Fl. Br. Ind. **5**: 286, 289–290. 1887), who excluded from the section all the species listed by Mueller (DC. Prodr. **15**(2): 352–355. 1866) except those with fleshy fruits. Pax and Hoffmann (Naturl. Pflanzenf. **19c**: 64. 1931) have also accepted the section in this sense. Beille, on the other hand (Fl. Gen. L'Indo-Chine **5**: 572. 1927), has continued the usage of Mueller, without however showing any convincing distinction between sect. *Emblica* sensu Mueller and sect. *Paraphyllanthus*.

It appears to me that only by adopting the narrow circumscription can sect. *Emblica* be maintained. Hooker described three new species, and two others have more recently been proposed; but all of these appear quite similar to one another and to *P. emblica*. Possibly the populations belonging to this section should be interpreted as a single widespread, variable species native from India to Malaya and China.

The present classification of sect. *Emblica* is provisional, for it does not approach very near to any of the three other sections included in subg. *Cicca*. The arboreal habit and fleshy fruit are only superficial resemblances and do not indicate any close affinity, particularly since the fruit of *Emblica* is still fundamentally capsular, in contrast to the truly drupaceous fruits of sects. *Cicca* and *Aporosella*. Furthermore, the pollen grains of sect. *Emblica* appear to differ considerably from those of the other three sections.

In the present treatment sect. *Emblica* is retained within subg. *Cicca* primarily on grounds of convenience, for it does appear to fit here better than in any other West Indian subgenus. The natural relationships of sect. *Emblica* are doubtless with Indian species of the sect. *Paraphyllanthus* sensu Mueller, such as *P. polyphyllus*, *P. lawii*, and *P. columnaris*.

9. **Phyllanthus emblica** L. Sp. Pl. 982. 1753; Muell. Arg. in DC. Prodr. **15**(2): 352. 1866; Hook. f. Fl. Br. Ind. **5**: 289. 1887.
(PLATE XV, *figs. J–L*).

Myrobalanus emblica Bauh. Pinax 445. 1623.
Nili-camarum Rheed. Hort. Malabar. 1: 69, *pl. 38*. 1672.
Phyllanthus foliis pinnatis floriferis, caule arboreo, fructu baccato L. Fl. Zeyl. 158. 1747.
Emblica officinalis Gaertn. Fruct. 122–123, *pl. 108, fig. 2*. 1790.
Emblica grandis Gaertn. op. cit. 123.
Emblica arborea Raf. Sylva Tellur. 91. 1838.
Diasperus emblica (L.) O. Ktze. Rev. Gen. 2: 599. 1891.

A deciduous tree up to c. 15 m. high, with flaking bark; annotinous branches smooth or hirsutulous, terete or somewhat angled, greyish or brownish, 2 — 5 mm. thick, with internodes mostly 1 — 3 cm. long. Cataphylls inconspicuous, subpersistent, dark reddish brown, scarious and brittle; stipules triangular-ovate, c. 1.3 — 2 mm. long, 0.8 — 1.3 mm. broad, acuminate, margins entire or denticulate, ciliolate when young, subauriculate at the thickened base; blades basally convex and much thickened, attenuate-acuminate, c. 1.5 — 1.9 mm. long. Deciduous branchlets (5–) 10 — 25 (–30) cm. long, pale brown, furrowed, copiously hirsutulous, terete, sterile or floriferous (and then shorter), with (15–) 30 — 100 (–150) leaves, the internodes very much shorter than the imbricate leaves (i.e., mostly 1 — 3 mm. long); fertile branchlets with leaves greatly reduced in proximal floriferous portion. Leaves: stipules triangular, 0.8 — 1.5 mm. long, 0.3 — 0.5 mm. broad, apex attenuate, ciliolate, minutely denticulate, becoming dark reddish-brown and scarious. Petioles stout, 0.3 — 0.7 mm. long. Leaf blades smooth, chartaceous, linear-oblong, obtuse, slightly oblique and subcordate at the base, mostly 12 — 20 mm. long and 2 — 5 mm. broad (reduced leaves associated with flowers considerably smaller); above olivaceous, the midrib and laterals often raised and conspicuous, beneath greyish or brownish, the midrib raised, the laterals (4 — 7 on a side) straight, steeply ascending; margin firmly thickened and sometimes scarious, more or less inflexed or involute, the scarious tip of the blade more or less inflexed.

Monoecious; first few proximal nodes of floriferous branchlets barren, with leaves reduced to dark brown scarious cataphylls; succeeding nodes with green but reduced leaves subtending cymules of male flowers, followed by nodes each with a cymule of one central female flower and several lateral males, the reduced leaves of this vicinity grading into normal leaves; distal half of floriferous branchlets normally sterile, with typical leaves, less commonly the distal portion not developed.

Male flower: Pedicel glabrous, slightly thickened above, c. 1 — 2.5 mm. long (up to 4 mm. long ex Mueller). Calyx-lobes 6, oblong-obovate or spathulate, 1.2 — 2.3 mm. long, 0.5 — 1 mm. long, obtuse or rounded, convex above, entire or obscurely denticulate, membranous, yellowish white, the midrib unbranched or with a few inconspicuous branches. Disk-segments 6, clavate, crenulate, foveolate, c. 0.2 — 0.3 mm. across; or disk sometimes obsolete. Stamens 3; filaments completely united into a terete column (0.2–) 0.3 — 0.7 mm. high; anthers sessile atop the column but discrete, erect, oblong, minutely apiculate, 0.5 — 0.9 mm. long, 0.5 — 0.6

mm. broad; anther-sacs parallel, dehiscing vertically, discrete, the slits not confluent; pollen grains (ex *Broadway 5258*) subglobose, 17.5 — 19 μ in diameter, 4- or 5-colporate, the colpi short, not bordered.

Female flower subsessile, the ill-defined pedicel 0.5 mm. long or less. Calyx-lobes 6, oblong or spathulate, 1.6 — 2.5 mm. long, 0.7 — 1.3 mm. broad, obtuse or rounded at the tip, more or less obscurely denticulate, thicker than the male, the scarious margin ill-defined or obsolete. Disk urceolate, investing the ovary, up to c. 1 mm. high, 6-ribbed, the ribs alternate with the calyx-lobes and projecting as marginal fimbrillae, the rim often with smaller teeth between the projecting ribs. Ovary smooth, ovoid; styles rather fleshy, shortly connate at the base, c. 2.5 — 4 mm. long, ⅓-parted to bifid, the branches bifid, remaining terete or flattened and conspicuously dilated and petaloid, usually spreading and distally reflexed.

Capsule with a firm fleshy greenish white or yellowish white epicarp, c. 2.5 — 3 cm. in diameter when fresh, the endocarp (cocci proper) rather massive and thick-walled, c. 1 cm. in diameter, the cocci at length separating from the columella; columella trigonous, slender below the dilated apex, c. 7 — 8 mm. high. Seeds of the pair in each coccus more or less unequal; the smaller plano-convex, 3.9 — 4.3 mm. long, c. 2.5 mm. radially, c. 2 mm. tangentially; the larger asymmetrically trigonous (carinate on one side), c. 4.5 mm. long, 3.1 — 3.2 mm. radially, c. 3 mm. tangentially; seed-coat dark chestnut brown, smooth, at high magnification with close-set rounded slightly convex flecks.

TYPE: left undesignated. There appears to be no specimen of *P. emblica* in the Hermann Herbarium (BM), and indeed Linnaeus cited none in the "Flora Zeylanica." There is a sterile specimen, number 1105–11, in the Linnaean Herbarium (LINN), which is probably this species; it is marked "H U," presumably indicating that it was grown in the botanic garden at Upsala. However, in view of the taxonomic uncertainty with regards to the limits and subspecific variation of *P. emblica*, it seems unwarranted to designate either this specimen or such illustrations as those of Rheede as representing the holotype. Typification of this Linnaean species must await a thorough study of the entire sect. *Emblica*.

DISTRIBUTION: *P. emblica*, in the present inclusive (though not necessarily correct) sense ranges from India and Ceylon to Hainan, Borneo, and Java. Mueller's reports of the species from Japan and the Mascarene Islands appear to be based on cultivated specimens. In the West Indies *P. emblica* is found only in cultivation and shows no signs of becoming part of the spontaneous flora.

BERMUDA: Public Garden, St. George's, *Brown, Britton, & Wortley 1732* (GH, NY).

CUBA: PINAR DEL RIO: Pinar del Rio City, Finca del Obispo, *Ekman 18643* (S). HABANA: Habana, *Marie-Victorin 45025* (MT). LAS VILLAS: Soledad, *Jack 4246* (NY, S).

PUERTO RICO: MAYAGUEZ: Agricultural experiment station, Mayaguez, *N. L. & E. G. Britton 7441* (NY).

LESSER ANTILLES: GRENADA: Botanic station, *Broadway* (NY).
TRINIDAD: Botanic gardens, St. Ann's, *Broadway 5238* (MO, S).

This species, widely cultivated in tropical regions, is perhaps the most economically important in the genus. Because of the use of the fruits as a purgative, it was the first species of *Phyllanthus* to become familiar to Europeans; pharmacists knew it as "emblic myrobalan" in Medieval times. However, it is also of some value as a timber tree (Pearson & Brown, For. Ind. 2: 878–881. 1932), and as a source of tannin (Burkill, Dict. Econ. Prod. Mal. 1: 920. 1935).

The great variability of the species is apparent even from the small sample of West Indian specimens, on which the description is mainly based. Both Mueller and Hooker reported the disk as absent in the male flowers, but in two of the flowering collections from the West Indies it is well developed as in the floral illustration of Wight (Icon. Pl. Ind. Or. **5**: *pl. 1896*. 1852). The fruit of the tree in the garden at Soledad, as observed from both herbarium (*Jack 4246*) and fresh material, is at least 2.5 cm. in diameter, which is much larger than that allowed by Hooker and better matches his *Phyllanthus pomiferus* [*Cicca macrocarpa* of Kurz]. The pollen grains of *Jack 4246*, not included in the description because they seem abnormally wrinkled, are subprolate, measuring c. 21 — 23 by 19 — 21 μ, and appear all to be 5-colporate.

The West Indian specimens appear to deviate from the norm of *P. emblica* somewhat in the longer branchlets with often an unusually large number of leaves. In *Broadway 5238* many of these long sterile branchlets are associated at a node with an abbreviated floriferous branchlet in which the distal leafy portion has been suppressed; such a marked dimorphism between fertile and sterile branchlets appears, however, to be rare. The fascicled branchlets which account for part of the characteristic appearance of the branches of *P. emblica* are, on close inspection, invariably found to be grown out from several collateral buds at a node from which the branchlet of the previous year has fallen.

Despite all these deviations, however, the West Indian collections show a close agreement in the apiculate anthers, unusual hypogynous disk, branchlet structure, and leaves; it therefore appears likely that they represent only variations of a single species.

(*To be continued*)

PLATE XV

LEAVES, MALE FLOWERS, AND FEMALE FLOWERS IN SUBG. *Cicca*.[13]

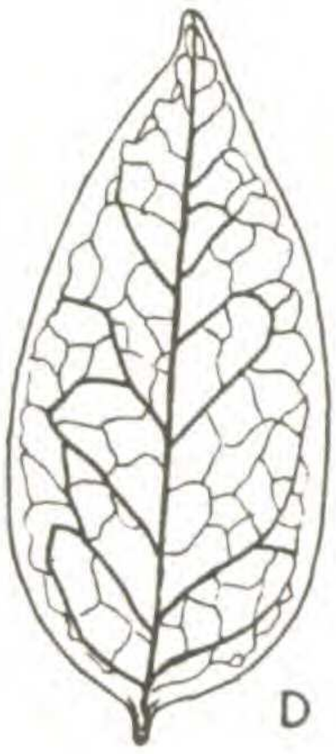
FIGS. A–C. *Phyllanthus pseudocicca* Griseb. (*Clemente & Alain 4079* [MICH]). FIGS. D–F. *Phyllanthus acidus* (L.) Skeels (cult., Kingston, Jam.). FIGS. G–I. *Phyllanthus elsiae* Urb. (G, H, *Matuda 16274* [US]; I, *Palmer 595* [GH]). FIGS. J–L. *Phyllanthus emblica* L. (J, K, *Broadway 5238* [S]; L, *Tsui 118* [A]).

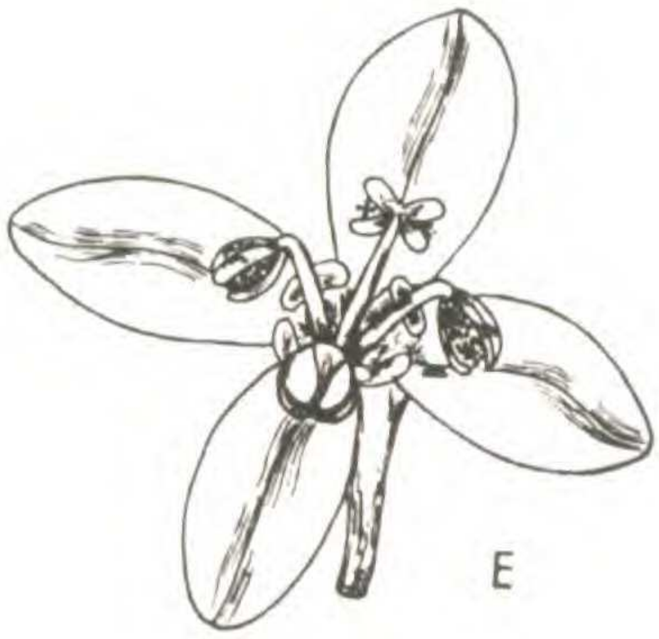
[13] Male and female flowers are drawn to the same scale.

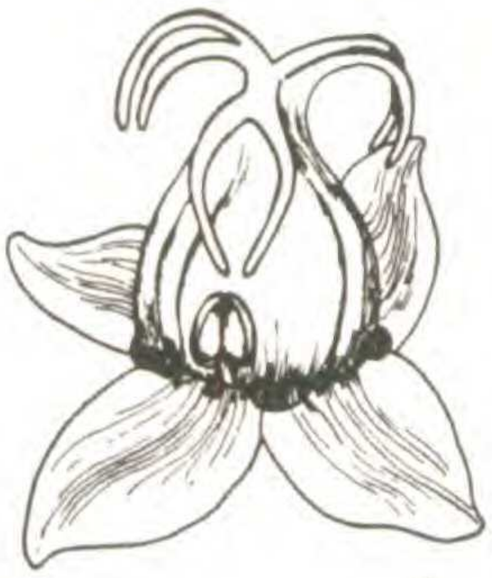

A


B

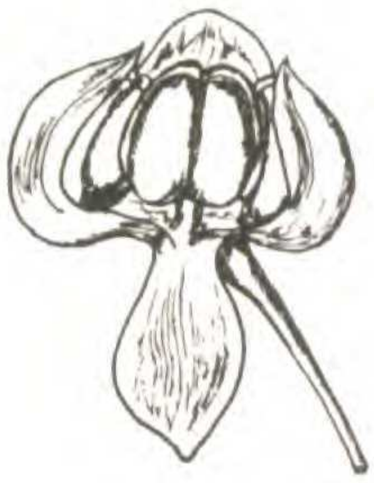

C


D


E


F


G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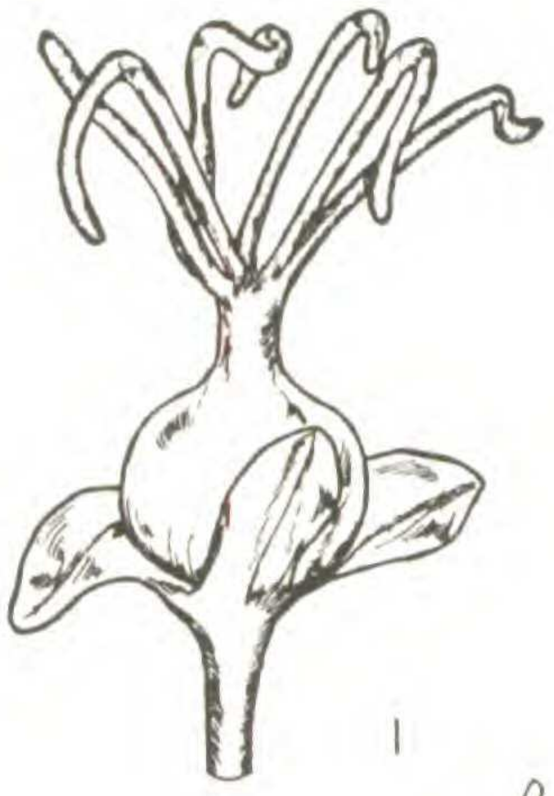
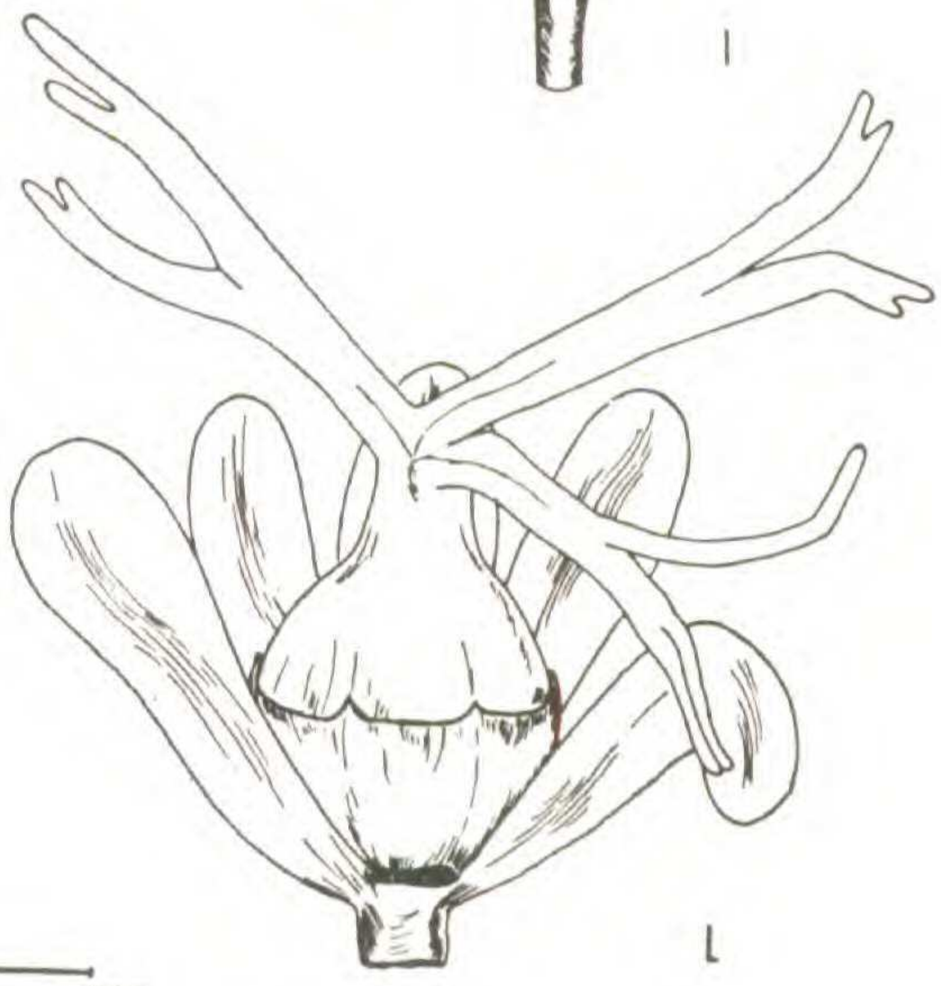

I


J


K


L

0 1 cm.

0 1 mm.

WEBSTER, WEST INDIAN PHYLLANTHUS